SEXUAL INTERFERENCE IN STUMPTAIL MACAQUES *(MACACA ARCTOIDES)*: IS IT RETURN-BENEFIT SPITE?

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For my parents and brothers

Soap and education are not as sudden as a massacre, but they are more deadly in the long run.

Mark Twain

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ABSTRACT

The phenomenon of intervening with other's matings, or sexual interference, was studied in a free-ranging group of stumptail macaques *(Macaca arctoides)*. This thesis suggests that its function may be immediately spiteful, but also ultimately beneficial reproductively. Preliminary evidence in support of this contention is presented, and speculations on related questions are offered. A proposed evolutionary scenario of the stumptail macaque mating pattern is also outlined.

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CHAPTER 1

INTRODUCTION

RATIONALE

Sexual interference as a topic of study within the field of animal behaviour, particularly in the context of evolutionary theory, is important. Not only does it centre around mating behaviour, which is necessary for mammals to reproduce, but it may be partially responsible for how privileges of mating and reproduction are allocated among competitors.

The ultimate purpose of sexual interference, defined as intervening with other's matings, is generally assumed to detract from reproduction (Arnold, 1976). In most species where it occurs, the behaviour can probably be classified as selfish in that the primary motive may be to improve one's own reproductive fitness over that of another's. However, in stumptail macaques *(Macaca arctoides)*, interference may actually be spiteful. It is the phenomenon of sexual interference in this species and in this context that serves as the focus for the present research.

OBJECTIVES

Accordingly, the primary objectives of this study are to begin to assess and test the following hypotheses:

(1) Whether sexual interference in stumptail macaques inflicts stress,

(2) is tactically spiteful, and

(3) is ultimately beneficial reproductively.

CHAPTER SUMMARIES

Chapter 2 reviews the literature on sexual interference in species where it has previously been recorded. It begins with insects and ends with humans, and shows how varied interference can be. It is meant to be informative, but not inclusive.

Following this, the next two chapters address logistics. Chapter 3 provides a brief background on the study species and the study area. Chapter 4 identifies the subjects and outlines the kind of data collected, when it was collected, how, and why.

Chapter 5 then provides a theoretical basis form which sexual interference in stumptails may be explained. It briefly reviews sexual selection and sociobiology.

Four results chapters follow. Chapter 6 begins by reviewing socio-sexual behaviour in the genus *Macaca*, and then describes the unique character of stumptail sexuality, before presenting the results on mating and comparing these with the studies of others. Similarly, Chapter 7 presents the results on the behaviour of sexual interference. It also describes its basic pattern among stumptails, as well as compares the results with other

studies.

Assessment of data occurs in Chapters 8 and 9. After considering other hypotheses, Chapter 8 proposes that sexual interference may inflict stress, and this may be best considered tactically spiteful, rather than selfish. Preliminary data are presented, followed by predictive tests and discussion. Chapter 9 then proposes that interference, when combined with alternative mating, may become spite with a return-benefit. More preliminary data are offered in support of this and predictive tests are presented and discussed.

Finally, Chapter 10 speculates about some further questions pertinent to sexual interference in stumptails, particularly the free-ranging subjects of the present study. It then outlines an evolutionary scenario of the stumptail mating pattern, placing interference in what is proposed is its proper context. The scenario is not, nor is the thesis, for that matter, put forward as absolute. Both are meant to serve as a guide for further research which will hopefully lead to an ultimate understanding of the significance of sexual interference in stumptail macaques. The chapter concludes by simply listing what was found in this free-ranging study not previously known from projects in captivity, emphasising the need for future empirical research.

CHAPTER 2

STUDIES OF SEXUAL INTERFERENCE

Within the Order Primates, sexual interference as a behavioural phenomenon is widespread. It is also common in both invertebrates and other vertebrates. For proper background and a survey of its variation, this chapter will review studies where sexual interference has been reported. Specific studies where it has served as the primary research focus will also be discussed. Table 2.1 provides a summary. For other reviews among primates, see Brereton (1976), Niemeyer (1980), and Niemeyer and Anderson (1983).

DESCRIPTIVE OVERVIEW

What follows is a brief review of sexual interference from other studies. It starts with insects and ends with humans, and represents an unsystematic review of the literature.

Invertebrates

Insects

Most male insects have prehensile apparatus such as hooks and spines designed for clasping. Male legs and antennae in many species are also

TABLE 2.1. Summary of sexual interference among animal species.

Animal Taxa	Common Name	Species	Perpetrator	Source
Insect	Dung Fly	*Scatophaga stercoraria*	Adult Males	Parker, 1970a, 1970b, 1974, 1978; Borgia, 1980
"	Solitary Bee	*Nomadopsis puellae*	"	Rutowski and Alcock, 1979
"	Anthocorid Bug	*Xylocoris maculipennis*	"	Carayon, 1974
"	Longicorn Beetle	*Rhagium bifasciatum*	"	Michelsen, 1962
"	Milkweed Beetle	*Tetraopes tetraophthalmus*	"	McCauley, 1982
Fish	Longear Sunfish	*Lepomis megalotis*	Adult Males/Females	Keenleyside, 1972
"	Bluegill Sunfish	*Lepomis macrochirus*	Adult Males/Females	Dominey, 1980, 1981; Gross, 1982
"	Honey Gourami	*Colisa chuna*	Adult Males	Janzow, 1982
Amphibian	Red-Spotted Newt	*Notophthalmus viridescens*	"	Verrell, 1982
"	Smooth Newt	*Triturus vulgaris*	"	Verrell, 1984
"	Tiger Salamander	*Ambystoma tigrinum*	"	Arnold, 1976
"	Common Toad	*Bufo bufo*	"	Davies and Halliday, 1979
Reptile	Iguanid	*Anolis lineatopus*	Adult Males	Rand, 1967
Bird	Prairie Chicken	*Tympanuchus cupido*	"	Robel and Ballard, 1974
Rodent	Ground Squirrel	*Spermophilus tridecemlineatus*	"	Schwagmeyer and Brown, 1983

TABLE 2.1. Continued.

Animal Taxa	Common Name	Species	Perpetrator	Source
Artio-dactid	Bighorn Sheep	*Ovis canadensis*	Adult Males	Geist, 1971; Hogg, 1984
Carnivore	Dwarf Mongoose	*Helogale parvula*	Alpha Female	Rood, 1980
"	Spotted Hyena	*Crocuta crocuta*	Subadult Males	Frank, 1986
"	Wolf	*Canis lupis*	Alpha Male/Female	Zimen, 1976, 1981
Pinniped	Elephant Seal	*Mirounga angustirostris*	Dominant Males	Le Boeuf, 1972, 1974; Cox and Le Boeuf, 1977
Elephant	African Elephant	*Loxodonta africana*	Adult Males Adult/Subadult Females Immatures	Dublin, 1983; Douglas-Hamilton, 1975; Short, 1966
Primate	Ringtail Lemur	*Lemur catta*	Adult Males Adult/Subadult Females Juveniles	Jolly, 1967
"	Bushbaby	*Galago crassicaudatus*	Adult Females	Roberts, 1971
"	Common Marmoset	*Callithrix jacchus*	Dominant Males/Females Adult Offspring	Abbott, 1984; Abbott and Hearn, 1978; Epple, 1975; Rothe, 1975
"	Brown Capuchin	*Cebus apella*	Alpha/Beta Males	Jason, 1984
"	Howler Monkey	*Alouatta palliata*	Adult Females Infants	Baldwin and Baldwin, 1973; Young, 1981; Jones, 1983

TABLE 2.1. Continued.

Animal Taxa	Common Name	Species	Perpetrator	Source
Primate	Squirrel Monkey	*Saimiri sciureus*	Adult Males Non-Oestrous Females Juveniles	DuMond, 1968; Baldwin, 1968
"	Spider Monkey	*Ateles belzebuth*	Juvenile Female	Klein, 1971
"	"	*Ateles geoffroyi*	Adult Females Juveniles	Klein, 1971
"	Common Langur	*Presbytis entellus*	Adult Males/Females Subordinate Males Subadults Juvenile	Jay, 1963; Yoshiba, 1968; Hrdy, 1974, 1977; Vogel, 1971
"	Nilgiri Langur	*Presbytis johnii*	Offspring	Poirier, 1970
"	Vervet Monkey	*Cercopithecus aethiops*	Dominant/ Juvenile Males Infants	Struhsaker, 1967b; Henzi and Lucas, 1980
"	Blue Monkey	*Cercopithecus mitis*	Juveniles	Tsingalis and Rowell, 1984
"	Sykes Monkey	*Cercopithecus albogularis*	Dominant Females Juvenile Males	Rowell, 1971
"	Red Colobus Monkey	*Colobus badius*	Adult Males	Struhsaker, 1975; Struhsaker, and Leland, 1985
"	Grey-Cheeked Mangabey	*Cercocebus albigena*	Subadult Male	Wallis, 1983
"	Patas Monkey	*Erythrocebus patas*	Adult/ Juvenile Males/Females	Hall, 1966; Loy and Loy, 1977; Harding and Olson, 1986

TABLE 2.1. Continued.

Animal Taxa	Common Name	Species	Perpetrator	Source
Primate	Japanese Macaque	*Macaca fuscata*	Dominant Males Juveniles Infants	Hanby et al., 1971; Stephenson, 1975; Huffman, 1984; Hanby and Brown, 1974
"	Rhesus Macaque	*Macaca mulatta*	Dominant/ Subordinate Males Adult Females	Wilson, 1981; Carpenter, 1942; Chapais, 1983; Ruiz de Elvira and Herndon, 1986
"	Stumptail Macaque	*Macaca arctoides*	All Age/Sex Groups	Niemeyer, 1980; Niemeyer and Chamove, 1983; Gouzoules, 1974; Estep et al., 1984 Bruce, 1982, 1984; Bertrand, 1969; Brereton, this study
"	Crabeating Macaque	*Macaca fascicularis*	Dominant Males Juveniles Infants	de Benedictis, 1973; Gore, 1986; Wheatley, 1982
"	Tonkean Macaque	*Macaca tonkeana*	Adult Males/Females Juveniles Infants	Thierry, 1986
"	Bonnet Macaque	*Macaca radiata*	Dominant Males	Rahaman and Parthasarathy, 1969
"	Barbary Macaque	*Macaca sylvanus*	Alpha Males	Burton, 1972
"	Pigtail Macaque	*Macaca nemestrina*	Alpha Male	Tokuda et al., 1968
"	Crested Macaque	*Macaca nigra*	Infants	Dixson, 1977

TABLE 2.1. Continued.

Animal Taxa	Common Name	Species	Perpetrator	Source
Primate	Olive Baboon	*Papio anubis*	Adult Males/Females Juveniles	DeVore, 1965; Hall and DeVore, 1965, Rowell, 1969 Smuts, 1985; Ransom, 1981
"	Yellow Baboon	*Papio cynocephalus*	Adult Males	Hausfater, 1975; Rowell, 1967
"	Gelada Baboon	*Theropithecus gelada*	Adult Females	Mori, 1979
"	Gibbon	*Hylobates lar*	Female Infant	Brody and Brody, 1974
"	Orangutan	*Pongo pygmaeus*	Juveniles Infants	MacKinnon, 1974; Galdikas, 1979
"	Chimpanzee	*Pan troglodytes*	Adult/ Subadult Males/Females Juveniles Infants	Tutin, 1975, 1979; Van Lawick-Goodall, 1968; Goodall, 1986; Ghiglieri, 1984; de Waal, 1982; Tutin and McGinnis, 1981; King et al., 1980; Nishida, 1979, 1983; Tutin and McGrew, 1973
"	Pygmy Chimpanzee	*Pan paniscus*	"	Thompson-Handler et al., 1984; Savage-Rumbaugh and Wilkerson, 1978
"	Gorilla	*Gorilla gorilla*	Dominant Male Adult Females Subordinate Males	Harcourt et al., 1980; Harcourt et al., 1981; Fossey, 1982; Hess, 1973
"	Human	*Homo sapien*	Adult Males	Shternberg, 1933; Lambert, 1966; Muller, 1917; Elwin, 1939; Maquire, 1928

highly modified. A likely explanation for these designs is prevention of displacement while mating (Richards, 1927). Not surprisingly, then, sexual interference among insects often occurs.

Among dung flies *(Scatophaga stercoraria)* (Parker, 1970a, 1970b, 1974, 1978; Borgia, 1980), a male, if he has not already located an uncourted female, will often try to dislodge another male already in copula. If successful, he will then copulate with the female himself. In this species, the last male to mate displaces most of the sperm left by others, and it is he who fertilises up to 80% of the eggs (Parker, 1978; Borgia, 1980).

In solitary bees *(Nomadopsis puellae)*, attempts by unattached males to dislodge copulating pairs are also common (Rutowski and Alcock, 1979). The standard procedure is for a male, while foraging for nectar, to locate and mate with a foraging female. As the day progresses, however, the number of males searching for females greatly increases. Competition for mates also increases, resulting in patrolling males striking copulating pairs. The attempt of the intruder appears to be to take over the female by usurping the courting male.

A highly unusual form of sexual interference has been recorded for the anthocorid bug *Xylocoris maculipennis* (Carayon, 1974). In this species, normal mating is usually achieved by the male puncturing the side of the female with his genitalia and simply injecting his sperm. On occasion, however, one male will inject another male. When this occurs, sperm from the injecting male enters the victim's testes only to be later reinjected into a female upon mating. Sexual interference takes place when homosexual insemination of one male by another occurs while the second male copulates heterosexually.

In at least two species of beetles, *Rhagium bifasciatum* and *Tetraopes tetraophthalmus*, sexual interference also occurs (Michelsen, 1962;

McCauley, 1982). The males of both species have occasionally been observed trying to dislodge other males in copula. Some attempts are successful; others are not. In the latter instance, the females involved often fly off while the fighting continues between the males. The copulating *Rhagium bifasciatum* males do not overtly resist. Their only response is to grasp the female more tightly. In the encounters noted, none of the intruding males succeeded.

Vertebrates

Fish

Among territorial sunfish *(Lepomis macrochirus)*, intrusions during spawning are common (Keenleyside, 1972; Dominey, 1980, 1981; Gross, 1982). The typical pattern of reproduction in this species is for a parental male to build a nest, attract a female, spawn, and then remain behind after the female's departure to protect the eggs until they hatch. Since non-parental males are much smaller in size and much less aggressive than parentals, they normally do not hold nesting territories. Instead, they use one of two alternative strategies. These are sneak and satellite, the latter also referred to as mimic. Sneakers dart from hiding places into nests of parentals when a female is present, presumably releasing sperm as they quickly dart off. The release of sperm is assumed since none is actually observed. Instead of darting in and out, the strategy of satellite males is to descend slowly into a nest from above while imitating female behaviour. They then begin releasing sperm when they are in proximity with the female. The parental males behave as if they are spawning with two receptive females. Unless detected and chased off by parentals, satellites remain until they have completed spawning. In addition, although uncommon, parental males and females intrude on the spawning of

others. When they do, the males release sperm before darting back to their own nests, while the females eat the opposing females' eggs.

Another example of sexual interference in fish comes from the anabantid species *Colisa chuna* (Janzow, 1982). In this species, as in *Lepomis macrochirus*, territorial males construct nests, attract females, spawn, and defend the boundaries of their territory. Non-territorial males, however, do not have the same opportunity. They instead use sneaking as their strategy, similar to the example of sunfish sighted above.

Amphibians

According to Verrell (1982, 1984), red-spotted and smooth newts *(Notophthalmus viridescens* and *Triturus vulgaris)* typically have a high-gain reproductive strategy (Dunbar, 1982). Males in both species court females by performing one of several stereotypic displays. Regardless of the pattern, however, the female usually ends up nudging the male's tail with her snout causing him to release spermatophore. A portion of the spermatophore is then taken into by the female's cloaca as she passes over it.

But Verrell only recorded sexual interference in both species in the side-payment strategy (Dunbar, 1982). As one male begins courting a receptive female, and just prior to having his tail nudged by her, a rival male approaches, places himself between them, and then touches the tail of the courting male in place of the female. The courting male deposits his spermatophore as usual, but the female is not in a position to receive it. Instead, she is positioned behind the rival male who's tail she begins to nudge. The rival male then deposits his spermatophore over which the female passes. She may or may not ultimately receive a portion of the courting male's spermatophore, but does receive most of the rival male's

deposit.

Red-spotted males are also known to mate by force when females are unreceptive. During these episodes, rival males often interfere by trying to squeeze between the pair. The courting male usually responds by attempting to shake off the rival before swimming away after the female.

In the tiger salamander *(Ambystoma tigrinum)*, rival males often place themselves between courting pairs and carry forth just as in newts (Arnold, 1976). The result is very low or no female contact with courting male's spermatophore.

Toads provide another example where interference commonly occurs. In the species *Bufo bufo*, males obtain females by either courting or by displacing already paired males (Davies and Halliday, 1979). During an episode of displacement, a rival male, if he is able to place a hold on a courting pair, will attempt a takeover by either sitting on top of the female in front of the courting male and pushing him with his hindlegs, or by squeezing between the pair from behind and nudging the courting male forward with his head. Whichever method the rival uses, if successful, he has most likely improved his own reproductive output while decreasing his competitors, all in one effort.

Reptiles

Concerning reptiles, Rand (1967) witnessed an episode of sexual interference in the iguanid species *Anolis lineatopus*. As a male was holding a female by the neck in the terminal stages of courtship, a rival male suddenly appeared in a bush nearby. After bobbing briefly, he jumped toward the pair terminating their copulation.

Birds

During observations of the greater prairie chicken (*Tympanuchus cupido*), Robel and Ballard (1974) recorded instances where copulations were disrupted by neighbouring males. These instances were relatively few during their 1969 field season. In 1970 and 1971, however, after the removal of three dominant males, these episodes increased dramatically. Evidently, according to Robel and Ballard, a highly stable social organisation among the males may be required to prevent sexual interference from occurring.

Mammals

Rodents

Among mammals, sexual interference in ground squirrels (*Spermophilus tridecemlineatus*) has also been recorded (Schwagmeyer and Brown, 1983). Males were observed disrupting the matings of others at a rate of .28 per hour of female oestrus during the 1978 field season. With a subsequent decline in the amount of sexual activity in 1979, this rate dropped to zero. This was interpreted as a result of reduced intrasexual competition between males.

Artiodactids

Disruption of matings in bighorn sheep (*Ovis canadensis*) is also common (Geist, 1971; Hogg, 1984). Breeding males are often challenged by other males for access to oestrous females. If a rival is successful in getting past a courting male's defences, usually after several minutes of butting, shoving and outright manoeuvring, he will quickly attempt to mate with the female before the courting male regains his position. If still mounted, he is promptly butted off. The process then begins again or the

challenge ends.

Carnivores

In the dwarf mongoose *(Helogale parvula)*, it is the alpha female who sexually interferes with the matings of the alpha male (Rood, 1980). She does this when his interest in her begins to wane and he starts mounting subordinate females. She then mounts him simultaneously.

Among spotted hyena *(Crocuta crocuta)*, subordinate males occasionally interfere with the matings of the alpha pair (Frank, 1986). Even though this behaviour is tolerated in young males, older males are usually driven off by the alpha male.

Wolves *(Canis lupis)* sexually interfere as well (Zimen, 1976, 1981). Since the alpha pair are normally the only individuals in a pack to reproduce, all mating attempts by both male and female subordinates are curtailed. If subordinates were to mate and were subsequently discovered by an alpha member, they would be subject to violent attack.

Pinnipeds

Sexual interference among elephant seals *(Mirounga angustirostris)* is well known (Le Boeuf, 1972, 1974; Cox and Le Boeuf, 1977). Males are harem breeders, and their ability to monopolise females is dictated by high dominance rank. High rank, therefore, determines their success in reproduction. Harem males usually prevent subordinates from approaching females, but, if they do, any attempts at mating are interrupted. The likelihood of high-ranking males in preventing subordinates from mating is also determined by a female's willingness to protest. Harem males interrupted the copulations of subordinates in 61.4% of the attempts in which females vocalised loudly. Only 25% of the subordinates' matings

were interrupted where the females remained silent or only partially protested.

Elephants

Sexual intrusions in the African elephant *(Loxodonta africana)* are somewhat different (Dublin, 1983; Douglas-Hamilton, 1975; Short, 1966; Poole, 1987). Since copulations usually last for less than a minute, little time is available for group members to interfere. Instead, what often happens is general herd excitement consisting of orienting toward the pair, ear flapping, screaming, trumpeting, rumbling, and spinning, while urinating and defecating. This behaviour occurs each time a new mounting begins. Furthermore, it is common for subordinate males to wait on the periphery for an opportunity to mate with the female themselves. Males in musth, who dominate most of the mating, also battle over oestrous females.

Primates

Prosimians

In ringtail lemurs *(Lemur catta)*, adult males do most of the interfering (Jolly, 1967). The actual sexual interference appears to be a carry-over of competing for access to oestrous females. Courting males were observed dismounting and rebuffing their rivals. Adult and subadult females and juveniles of both sexes also sometimes interfere.

Roberts (1971) observed adult female bushbabies *(Galago crassicaudatus)* interfering with the copulations of others. Two females were noted to interfere with each others' matings in turn.

New World Monkeys

For common marmosets *(Callithrix jacchus)*, dominant males and

females disrupt the matings of subordinates (Abbott, 1984; Abbott and Hearn, 1978; Epple, 1975). Subordinate males appear to be the concern of the dominant males, while subordinate females the concern of dominant females. Also, while in family groups, adult offspring occasionally interfere with their parents' copulations (Rothe, 1975).

In brown capuchins *(Cebus apella)*, Jason (1984) witnessed sexual interference in the matings of both the alpha and beta males. If either had any lapses of attention while consorting with oestrous females, they would respond to attempts by subordinate males to mount their consorts by interfering and then chasing them off.

Howler monkeys *(Alouatta palliata* and *Alouatta caraya)* also exhibit sexual interference (Baldwin and Baldwin, 1973; Young, 1981; Jones, 1983). The Baldwin's observed an infant try to make contact with her mother each time she mated. Young recorded interference by an adult female, and Jones noted that mating pairs were interrupted by others, but did not identify the age or sex of the intruders.

Among squirrel monkeys *(Saimiri sciureus)*, adult males are the most common sexual intruders (DuMond, 1968; Baldwin, 1968). Whenever matings occurred between consorting pairs, non-participating males inevitably rushed to interact. Non-oestrous females and juveniles were observed to interfere as well.

Klein (1971) observed sexual interference in two species of spider monkeys *(Ateles belzebuth* and *Ateles geoffroyi)*. For the former species, a juvenile female was once observed to actively swing above the heads of a pair while they copulated. Two other adult females were in association, but neither intruded. In the latter species, both juveniles and adult females interfere. Even though Klein described these episodes as playful, the courting male would occasionally dismount to rebuff his adversaries.

Old World Monkeys

Reports of sexual interference among Old World monkeys are probably the most common. In langurs (*Presbytis entellus* and *Presbytis johnii*), most age and sex classes seem to participate. According to Jay (1963), copulating pairs are often encircled by threatening juveniles, subadults, and adult males. Yoshiba (1968) witnessed interference by subordinate males, but also by adult females. Hrdy (1974, 1977) observed intrusions by male and female juveniles, subadults, and adults, while Vogel (1971) observed dominant male intrusion. In the one mating recorded by Poirier (1970), the courting female's offspring interfered.

Vervet monkeys *(Cercopithecus aethiops)* provide another example of Old World primates in which sexual interference has been observed (Struhsaker, 1967b; Henzi and Lucas, 1980). The most common intruders seem to be dominant and juvenile males, and infants of both sexes.

Juvenile male and female Blue monkeys *(Cercopithecus mitis)* also sexually interfere (Tsingalia and Rowell, 1984). Occasionally, they disrupt matings entirely by physically pushing at the male until he is unable to remain mounted on the female.

Among Sykes monkeys *(Cercopithecus albogularis)*, Rowell (1971) observed interference by juvenile males and, sometimes, by dominant females. The intrusions by males often varied from tail-pulling to persistent attacks. Since the courting male would occasionally dismount to rebuff his rivals, it usually took him several attempts to successfully achieve intromission.

In the red colobus monkey *(Colobus badius)*, adult male aggression involves rival males interfering with the copulations of courting males (Struhsaker, 1975; Struhsaker and Leland, 1985). Matings often end

prematurely when this occurs.

Sexual interference in gray-cheeked mangabeys *(Cercocebus albigena)* appears to be minimal (Wallis, 1983). A subadult male was twice observed to circle an adult male and female pair while they mated. He also shook his head and was once observed to hit at the hindquarters of the courting male. Neither episode was retaliated against.

Interference among patas monkeys *(Erythrocebus patas)* is more common (Hall, 1966; Loy and Loy, 1977; Harding and Olson, 1986). Adult and juvenile males and females often interact with mating pairs. Generally, intrusions by adult females and juvenile males are the most intense. Displays usually consist of charging and threatening by females, while males charge, slap at, bounce off, and vocalise at the pair. These displays often lead to an increase in the courting male's number of mounts before ejaculating, though matings are occasionally terminated altogether.

In Japanese macaques *(Macaca fuscata)*, dominant males frequently interfere with the matings of subordinates (Hanby et al., 1971; Stephenson, 1975; Huffman, 1984; Hanby and Brown, 1974). Even though this often leads to the interruption of matings, it does not prevent courting pairs from mating again after interference ceases. Juveniles and infants also interfere, but less frequently.

Dominant male rhesus macaques *(Macaca mulatta)* interfere with the matings of others as well (Wilson, 1981; Carpenter, 1942; Chapais, 1983; Ruiz de Elvira and Herndon, 1985). Generally, their tendency is to chase the courting female, but they occasionally direct their interference toward the courting male, or both. Subordinate males and adult females rarely interfere. Regardless of who the intruders are, however, most copulatory series are not disrupted by interference.

Sexual interference among stumptail macaques *(Macaca arctoides)* is

very common (Niemeyer, 1980; Niemeyer and Chamove, 1983; Gouzoules, 1974; Estep et al., 1984; Bruce, 1982, 1984; Bertrand, 1969; this study). All age and sex classes are known to participate. In its mildest form, it consists of an individual approaching a copulating pair and sitting. More active forms include reaching toward the pair while teeth-chatter grimacing and, occasionally, hitting either the courting male or female. Interference in stumptails will be discussed in detail in later chapters.

The crabeating macaque *(Macaca fascicularis)* has also been observed to sexually interfere (de Benedictis, 1973; Gore, 1986; Wheatley, 1982). Dominant males intrude on occasion, but it is the juveniles and infants of both sexes that interfere with copulations most often, particularly those of their mothers.

According to Thierry (1986), it is infants and juveniles of both sexes that intrude most often among Tonkean macaques *(Macaca tonkeana)*. Adult females interfere less often, and intrusions by adult males occur only rarely.

Sexual interference by adult male bonnet macaques *(Macaca radiata)* is also rare. But Rahaman and Parthasarathy (1969) did observe dominant males intrude upon the copulations of subordinate males on four separate occasions.

Barbary macaques *(Macaca sylvanus)* show little interference as well (Burton, 1972). Alpha males do, however, occasionally disrupt the matings of subadult males during the breeding season.

Tokuda et al. (1968) observed an alpha male in a group of pigtail macaques *(Macaca nemestrina)* prevent subordinate males from mating by interfering.

In Crested macaques *(Macaca nigra)*, infants interfere in courting pairs' copulations by climbing on the female's back and clutching at the male

(Dixson, 1977).

Sexual interference among olive baboons *(Papio anubis)* is more common (DeVore, 1965; Hall and DeVore, 1965; Rowell, 1979; Smuts, 1985; Ransom, 1981). Adult males interfere most often, but adult females and juveniles of both sexes also occasionally intrude. According to Ransom, interference seems to increase the number of mounts a male requires to reach ejaculation.

The adult males among yellow baboons *(Papio cynocephalus)* also occasionally interfere (Hausfater, 1975; Rowell, 1967).

In gelada baboons *(Theropithecus gelada)*, it is the dominant female who disrupts the copulations of other adult females (Mori, 1979).

Apes

Sexual interference among apes is also common. In gibbons (*Hylobates lar*), the Brody's (1974) observed a female infant persistently interfere with all of the matings attempted by her parents.

Infant and juvenile orangutans *(Pongo pygmaeus)* also intrude in their mothers' matings (MacKinnon, 1974; Galdikas, 1979). Typically, this is done by biting, striking and pulling at the male.

Among chimpanzees *(Pan troglodytes* and *Pan paniscus)*, sexual interference is common. Adult and subadult males and females typically interfere, as do both sexes of juveniles and infants (Tutin, 1975, 1979; Van Lawick-Goodall, 1968; Goodall, 1986; Ghiglieri, 1984; de Waal, 1982; Tutin and McGinnis, 1981; King et al., 1980; Nishida, 1979, 1983; Tutin and McGrew, 1973; Thompson-Handler et al. 1984; Savage-Rumbaugh and Wilkerson, 1978).

In gorillas *(Gorilla gorilla)*, it is the dominant male that intrudes upon the copulations of others most often (Harcourt et al., 1980; Harcourt et al.,

1981; Fossey, 1982). Only rarely do adult females, subordinate males, and immatures interfere (Harcourt et al., 1980; Harcourt et al., 1981; Hess, 1973).

Humans

And finally, in humans *(Homo sapien)*, even though sexuality involves secrecy which makes sexual interference less likely (Bancroft, personal communication), there are cases where it has been indirectly documented in a preindustrial context (Daly et al., 1982). Each instance involves the discovery of an adulterous relationship of a wife by her husband or his accomplices. For example, among the Gilyak of Eastern Siberia, "a stranger caught in flagrante delicto with a married woman is slain at the scene..." (Shternbery, 1933:227). Two other examples where the retribution of murder is acceptable for committing adultery are among the Gilbertese and Yap peoples of Polynesia. Lambert (1966:653) noted that among the Gilbertese, "an adulterer caught in the act was killed immediately...". Among the Yap (Muller, 1917:229), a husband having caught his wife committing adultery, "...had the right to kill her and the adulterer or to burn them in the house".

Even if not murdered, the punishment for an adulterer can be severe. Among the Baiga of India, according to Elwin (1939:142), a woman remembers being entrapped by her husband with her lover whom he attacked with a blazing log. To punish her, he applied chilies to her vagina. Also, among the Masai of East Africa, Maguire (1928:116) noted, when referring to the case of the adulterous wife and her lover, the following: "Should he be caught in the act, the friends of the cuckold tie him up at the kraal door and he is beaten...".

Responses of wives to coitus of their adulterous husbands and children to

coitus of their adulterous or nonadulterous parents were not found.

SPECIFIC STUDIES AND FINDINGS

As can now be better understood, when considering the phenomenon of sexual interference among different species of animals, examples are not difficult to find. Far fewer, however, are examples of studies where interference has been specifically addressed. What follows is a brief review of these studies and their findings, most of which were mentioned earlier. As appropriate, the ideas of some will be briefly discussed in the beginning of Chapter 8.

Insects

Parker (1970b) studied sexual interference among yellow dung flies *(Scatophaga stercoraria)*. During the spring and autumn seasons of reproductive activity, it is common for males to search for gravid females as they approach fresh cow droppings to lay their eggs following mating. Competition between males for females is intense because males often outnumber females by as much as four to one during the height of the season. This commonly leads to "takeovers" where a male in copula or oviposition with a gravid female is attacked and displaced by a rival male. Oviposition is the period following mating that a female uses to deposit her eggs after the male ceases genital contact but remains mounted. It is referred to a the "passive phase."

In his study, Parker found that takeover attempts by rival males almost always led to reactions of rejection by courting males, and a struggle for the possession of the female would usually ensue. Even though two or more males may attempt a takeover simultaneously, a more typical sequence

involves a single rival trying to place himself between the courting pair by first mounting the courting male, forcing him to release his grasp of the female's thorax, and then displacing him by pushing him backwards. The courting male responds by standing and extending his middle legs to increase the distance and prevent the rival from gaining a grip on the female. He also typically responds, if in the passive phase, by trying to regain genital contact with the female as if to recopulate.

When successful, the rival male inevitably copulates with the female himself. If it is the original male who prevails, however, he either continues mating, or, if already in the passive phase, releases his regrasp of the female's abdomen before resuming oviposition. Of all the takeovers attempted by rival males, 1.75% were successful when the courting pair were in oviposition, while .65% were successful when they were in genital contact.

Parker concluded by suggesting that takeovers presumably are never to the selective advantage of females, but rather to males who can mate and fertilise a larger number of eggs then they would otherwise. And, as a deterrent to takeovers, the male's passive phase minimises egg loss. The factors that determine which males succeed were not addressed, but male size, vigour, and age were suggested as possibilities.

Fish

Sexual interference in fish has been studied as well. For example, Keenleyside (1972) observed interference in Northern longear sunfish *(Lepomis megalotis)*. In this species, colony breeding is typical. Not all males are territorial, but, during the spring and summer, most congregate along the edges of rivers to build their bowl-shaped nests in the substrate by using their tails. Anywhere from a dozen to several hundred of these nests

exist in a single colony. After they are built, each nest is then guarded against all other males. This continues throughout spawning and the hatching of the eggs.

When a sexually mature female enters the territory of a male, spawning begins. As the pair slowly circle, the female tilts periodically to release eggs, which the male promptly fertilises. The eggs then settle to the bottom of the nest until they hatch, while the male stands guard. Since pair formation is not prolonged, a male typically spawns with several females and often ends up guarding the eggs of more than one. It is also common for females to spawn with more than one male.

Sexual interference is most common during the tilting phase of spawning. As a female tilts to release eggs, a rival male, nest builder or not, darts in, briefly settles near the female, and then quickly dashes off. If detected by the resident male while intruding, he is chased off. Finally, when breeding activity is at its peak, several rival males typically intrude each time a female releases eggs.

Keenleyside suggests that an intruding male uses the brief period near a female to release sperm, resulting in an increase in his progeny. But, since females occasionally intrude as well, apparently to eat eggs, he also suggests that interference in this species is multi-functional.

A second study among fish was carried out by Gross (1982). His species of interest was the North American bluegill sunfish *(Lepomis macrochirus)*. Like longear sunfish, bluegills are colony breeders. Parental males typically construct lake bottom nests of 5 to 150, depending on the size of the colony. However, like longears, not all males construct nests. Sneaker and satellite males, who are not nest builders, differ in colour, are smaller in size, and gather on the periphery of colonies. As the time for spawning nears, gravid females approach the colonies in schools and then

separate to enter the nests individually, releasing eggs shortly thereafter with horizontal dipping motions. It is at these moments that sneakers intrude and release sperm. Satellites spawn with courting pairs by mimicking females. After spawning for several hours, the females leave for deeper water, while only the parental males remain to guard the eggs until hatching, which takes about seven days. Males then return to deeper water themselves until the process is begun again, usually within 10 days. Four to five of these sessions constitute a breeding season.

Gross concludes that the three behavioural types among males are actually different reproductive strategies. Compared with parental males, sneakers and satellites never become large enough to compete for nesting sites. They instead mature more quickly and gain spawning access by first sneaking, and then mimicking, after the approximate size of gravid females is reached. How males come to use any one strategy is unknown.

Amphibians

Two studies of sexual interference among amphibians also exist. Arnold (1976) studied tiger salamanders *(Ambystoma tigrinum)*, while Verrell (1984) studied smooth newts *(Triturus vulgaris)*.

In the tiger salamander, courtship behaviour starts with a tail-nudging walk. When within touching distance of a female, a courting male typically begins by suddenly turning away and pausing. He then uses his tail to monitor her position. If the female is receptive, she will turn in his direction and place her snout at the base of his tail. As she begins nudging in the vicinity of his cloaca, he moves forward and stops. If she continues to follow and nudge, he continues to move forward and deposit spermatophores. These deposits are then taken into her cloaca as she moves forward and passes over them.

Since courting males rely completely on touch, they are highly susceptible to sexual interference. It is common for rival males to intercede just prior to tail nudging so that the courting male is nudged by the rival, rather than the receptive female. At the same time, the rival begins tail monitoring the female who ultimately nudges his cloaca and receives his spermatophore. The deposit of the courting male is usually covered over or destroyed. To Arnold, this behaviour serves the double function of promoting the reproductive success of the rival while decreasing that of his competitor.

As described by Verrell, the courtship behaviour of the smooth newt is almost identical with that of the tiger salamander. Orientation begins as the male faces the female. If she is receptive, the female will approach after male tail display. When she does, the male moves backwards, continuing his display, as she continues to follow. The male deposits a spermatophore and turns to block the female's path when she touches the base of his tail with her snout. She comes in contact with the deposit as she moves forward to start the sequence again. Only after two or three of these sequences does the courtship end.

Of the 78 triadic encounters Verrell observed, 45 (58%) included sexual interference. Again, these occur much as they do in tiger salamanders. Just as the courting female begins to initiate spermatophore deposition from the courting male, a rival slips between them and takes her place. As he then nudges the tail of the courting male, his tail is nudged by the courting female who is appropriately situated to receive his spermatophore rather than that of his opponent.

According to Verrell, by using this strategy, rival males were responsible for 7 of 45 female inseminations, as well as two multiple inseminations where the female received a spermatophore from both males. He concluded

that sexual interference in smooth newts is a "side-payment" strategy (Dunbar, 1982) whereby males who use it benefit reproductively over those who use only the strategy of the courting male, also known as the strategy of high-gain (Dunbar, 1982).

Pinnipeds

Cox and Le Boeuf (1977) studied sexual interference among the elephant seals *(Mirounga angustirostris)* of Ano Nuevo Island, California. In this species, males typically fight amongst themselves for control of females during the breeding season which occurs from late December to mid March. According to Le Boeuf (1972), males arrive in early December and disperse along the beach according to dominance rank with the alpha male having access to all areas. Females do not start arriving until late December, and, as they do, they congregate at the centre of the beach in a tight pod. From the beginning of their arrival, the alpha male mates with as many of them as he can, keeping other males away. However, as their numbers increase, peaking around the first of February, less dominant males are able to mate on the pod's periphery. If they are caught, they are usually quickly interrupted by the alpha male or another male more dominant than themselves.

Active protests by the females often facilitate these interruptions. Protests are a female's general struggle to escape from a male suitor. Females threaten the male vocally, whip hindquarters vigorously from side to side, flip sand in the male's direction, and bite his neck. Cox and Le Boeuf found that of the 158 mounts protested for their entirety by oestrous females, 97 (61.4%) received interference. Small, young, low-ranking males were interrupted more quickly and more often. To account for this, Cox and Le Boeuf noted that the probability of males surviving to age 10

and beyond is quite low because of intense competition. Consequently, sexual interference functions to increase the harem male's reproductive fitness and is facilitated by female protest.

Primates

Specific studies of sexual interference among primates are more numerous. The first to be reviewed is by Young (1981). This study describes an instance of sexual interference among female howler monkeys *(Alouatta palliata)* on Barro Colorado Island in Panama. On 14 June 1974, Young observed an adult female actively disrupt the copulation of another by rapidly approaching and vocalising loudly. Both females then pushed at each other for about 30 seconds before the courting female separated and walked off. As she departed, the intruder sat down within a half meter of the male who had been sitting and watching. The male remained for approximately four minutes before he also turned and walked away. Young describes this incidence as a social mechanism for curbing population growth.

Loy and Loy (1977) also studied interference, but among a captive colony of patas monkeys *(Erythrocebus patas)* on La Parguera Island, Puerto Rico. During 781 hours of observation, they observed sexual interference on 59 occasions. Typically, it included orienting toward the mating pair while grabbing, slapping and vocalising. The individuals generally involved were immature males, but adult and immature females would also occasionally take part. The rate of participation for males was 86.4%, while for females it was 10.2%. Furthermore, even though there was little age difference between the sexes when displayed, immature males showed a higher interference frequency. Females averaged .001 acts of intrusion per hour for the first two years of life, while males increased from

.012 for the first year to 0.042 for the second. Immature males were also more disruptive. Of the 84 copulation attempts by courting pairs, 24 (28.6%) were terminated prematurely. Of these, immature males were responsible for all but one. Also, though intruders showed a preference for the same sex, adult males received the majority of aggression. Intruders directed their interference at the male in 25 (86.2%) of the 29 episodes where the individual of focus could by determined satisfactorily.

To explain this behaviour, the Loy's attribute the motivation of interference, particularity for immatures, to an "...excitatory effect of witnessing adult sexual interactions..." and to an "...approach/withdraw conflict experienced by the harasser once near the adult male." They also see "...dominance testing of the adult male by maturing males..." as the primary function.

Crabeating macaque *(Macaca fascicularis)* sexual interference behaviour has been documented in two studies. The first is by de Benedictis (1973), and the other more recent work is by Gore (1986). Both studies were carried out on captive groups and address sexual interference in immatures.

According to de Benedictis, individuals that intrude most often are unweaned infants. In addition, offspring attend the matings of their mothers more often than those of unrelated females. Proximity is possibly responsible for this tendency. Furthermore, of those that interfere between the ages of 0-12 months, males are more often involved than females since females pay little attention, remaining with their mothers. For intruders aged 12-24 months, the pattern for both sexes resembles that of younger males. Older infants also show an increased inclination to touch one or both of the copulating members. Since immatures display much "anticipatory excitement and imitation" during matings, de Benedictis attributes the developmental function of interference to be that of

observational learning.

In comparison, Gore found that infants interfere only with the matings of their mothers, ignoring the matings of others. Even though both sexes are equally involved, the pattern seemed to differ among sibships. Where one infant does or does not interfere, its sibling does the same. Gore concludes that interference among infants is a form of parent-offspring conflict. The finding that mounts per mother-male contact are greater when offspring are absent (.143) then when present (.076) confirms this (Walsh test, N=12, p=.005, 1-tailed). In other words, according to Gore, the function of infant interference is to delay conception, and, hence, sibling competition for resources.

Thierry (1986) studied sexual interference in an outdoor group of Tonkean macaques *(Macaca tonkeana)*. He found that intruders are typically males and females under five years of age, but adult females also occasionally interfere. The young individuals intrude most often upon their mothers' matings, particularly if they are from 2 to 3 years of age, while adult females interfere with the matings of related females more than unrelated. The tolerance level of courting males also seems to decrease as the ages of the intruding individuals increase. Thierry hypothesises that "...the third individual desires to be involved in the interaction, and its behaviour reflects the tolerance of the mounter." He also argues that this interpretation may be applied across primates.

A study of interference in an outdoor group of rhesus macaques *(Macaca mulatta)* was done by Ruiz de Elvira and Herndon (1986). They discovered that males were more active interrupters than females, and both, when involved, are of high dominance rank. Typically, intruding males are higher ranking than either member of the courting pair, while females out rank only the courting female. Disruptive interference is also most often

directed toward the courting female whom the courting male makes little effort to protect. Because of this, lower-ranking individuals tend to initiate matings while absent from view. Ruiz de Elvira and Herndon, therefore, suggest that the interdependence between mating activity and high rank discovered in other studies may be misleading.

Specific studies of sexual interference among captive stumptail macaques *(Macaca arctoides)* have been done by Gouzoules (1974), Niemeyer (1980; Niemeyer and Chamove, 1983), and Bruce (1982, 1984). Each will be reviewed in order. Gouzoules found that, unlike most primates, all age and sex classes commonly interfere, particularly juveniles and subadults. They feign indifference until the precise moment of ejaculation and then intrude. Depending on the individual and the circumstance, they usually react by teeth-chatter grimacing, by reaching toward the pair while teeth-chatter grimacing, or by teeth-chatter grimacing while touching, hitting at and circling the pair. Interference stops when the courting male terminates his expiration vocalisations at the end of the ejaculatory phase. The tie phase, or prolonged post-ejaculatory intromission, common in stumptails, has, by then, already begun. The male responds most often by threatening back while remaining tied. According to Gouzoules, interference serves to redirect courting male aggression from the mating female.

In Niemeyer's study, of the 271 recorded matings, 93% received interference. Again, individuals from each age and sex category participated. Young adult females were the most active, followed, in order, by infant females, young adult males, infant males, and adult females. Adult males interfered the least. A seven week old female infant was the youngest to intrude. No overall sex difference existed, but Niemeyer did find that dominant individuals interfere more often than individuals of lower rank. The courting males were also the receivers of most of the

interference. After testing three separate hypotheses (protective, reproductive and possessive), Niemeyer concluded that interference serves as a reproductive strategy only for dominant males, while other individuals interfere to reestablish bonds with courting females severed temporarily by mating.

In a third study on stumptails, Bruce found, after recording data on 618 matings, that females interfere more than males, the alpha male and high-ranking females are interfered with more often than lower-ranking individuals, and interference is more pronounced and tie durations longer when copulations are not interrupted by another male. Tie durations are also significantly longer when matings are interfered with than when they are not. Furthermore, interference is not influenced by either age, dominance, or kinship. Even though Bruce states that the function of interference is unclear, she suggests that it may serve as a release for group tension, dominance testing, or intermale reproductive competition.

To conclude, Tutin (1979) studied sexual interference in chimpanzees *(Pan troglodytes)* at Gombe National Park in Tanzania. Data on 1070 copulations demonstrated that immature males and females intrude the most, followed by adult males. Adult females interfered only twice. Tutin also found that, when infants choose to intrude, they interfere with the matings of their mothers, while juvenile males interfere with the matings of unrelated females. Adult males interfere only when possessive. Tutin considers interference to be the result of weaning duress among infants, early developmental possessiveness among juvenile and adolescent males, and reproductive competitiveness among adult males.

SUMMARY

This chapter demonstrates that sexual interference is a common phenomenon among animals (Table 2.1). In most species where it occurs, it appears to be one form of adult male-male reproductive competition. However, in mammals, sexual interference may be this and more, since adult females also commonly interfere. In primates, subadults and immatures interfere as well, particularly in stumptail macaques. Attention now will shift to the present study to attempt to explain sexual interference in this species.

CHAPTER 3

RESEARCH SETTING

With the aims of the research defined and the topic of sexual interference reviewed, this chapter will present a general background on stumptail macaques and an overview of the research site.

TAXONOMY OF STUMPTAIL MACAQUES (*MACACA ARCTOIDES*)

Within the Order Primates, stumptail macaques are included among the Superfamily Cercopithecoidea, the Family Cercopithecidae, and the Subfamily Cercopithecinae (Figure 3.1). Their genus is *Macaca*, species *arctoides*, and common name stumptail (or bear) macaque (Figure 3.1) (Wolfheim, 1983; Hill, 1974). Previously classified as *M. speciosa* (Blyth, 1875), the classification suggested by Geoffroy Saint-Hilaire (1831) is the species name now generally accepted (Fooden 1967, 1971, 1976, 1980; Medway, 1970; Napier and Napier, 1967, 1985; Thorington and Groves, 1970; Wolfheim, 1983; Hill, 1974). Stumptail phylogeny is not totally understood, but they are believed to be the only species within one of four macaque species groups (Figure 3.1). They are placed in their own group because both males and females have unique genitalia (Fooden, 1976, 1980). The species of macaque to which they are most closely

FIGURE 3.1. Taxonomy of the genus *Macaca* (adapted from Fooden, 1976, 1980; Napier and Napier, 1985).

Order:	Primate			
Suborder:	Anthropoidea			
Infra-Order:	Catarrhini			
Superfamily:	Cercopithecoidea			
Family:	Cercopithecidae			
Subfamily:	Cercopithecinae			
GENUS:	*MACACA*			
Species Group:	*M. Silenus-Sylvanus*	*M. Fascicularis*	*M. Sinica*	*M. Arctoides*
Species: (Common Name):	*M. silenus* (Liontail)	*M. fascicularis* (Crabeating)	*M. sinica* (Toque)	*M. arctoides arctoides* * (Stumptail)
	M. sylvanus (Barbary)	*M. fuscata* (Japanese)	*M. assamensis* (Assamese)	
	M. maurus (Moor)	*M. mulatta* (Rhesus)	*M. radiata* (Bonnet)	
	M. nemestrina (Pigtail)	*M. cyclopis* (Taiwan)	*M. thibetana* (Thibetan)	
	M. ochreata (Booted)			
	M. nigra (Crested)			
	M. tonkeana (Tonkean)			

*= The other three subspecies of the *M. arctoides* species group are *M. arctoides melanota*, *M. arctoides melli*, and *M. arctoides subfossilis*. Each is recognised by subtle differences in anatomy resulting from local geographic isolation (Hill, 1974).

related is uncertain (Eudey, 1980).

STATUS

Geographic

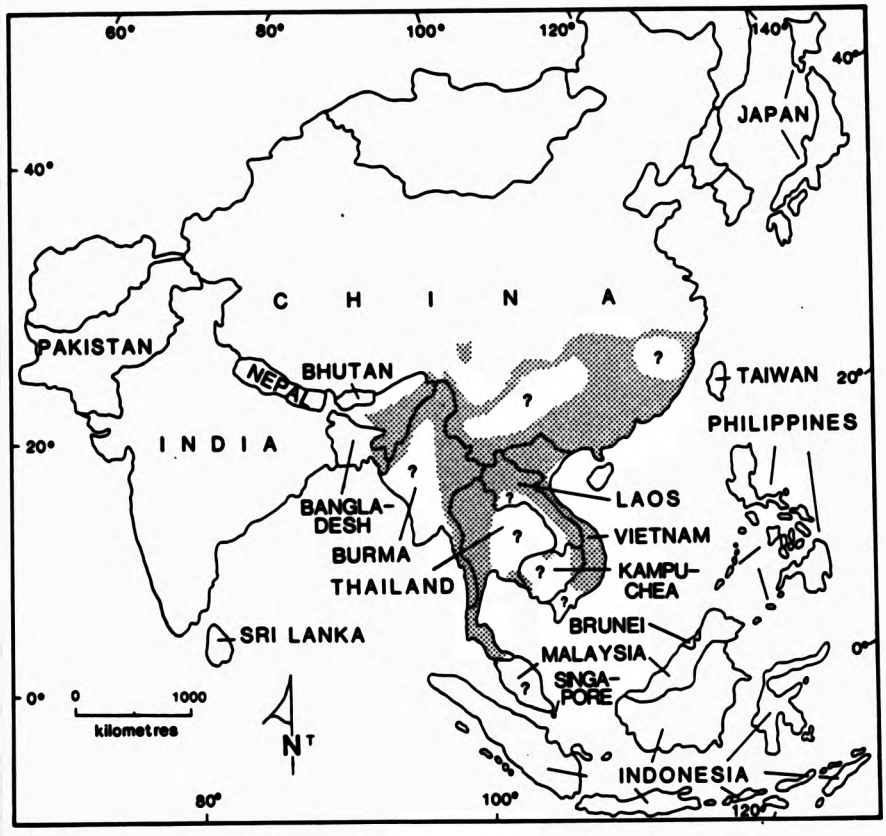
In their natural setting, stumptail macaques are sporadically distributed throughout continental Asia between 6° to 31° N latitude and 92° to 115° E longitude (Figure 3.2) (Wolfheim, 1983; Eudey, 1980; Fooden, 1976; Hill, 1974). This area extends from northern peninsular Malaysia in the south to southern China in the north, and from parts of eastern India and southeastern Blangladesh in the west to Vietnam and eastern China in the east. The presence of stumptail macaques in southwestern Burma, southern Laos, eastern Thailand, central and southern Kampuchea, the southern tip of Vietnam, and certain inclusive areas in China is unknown (Figure 3.2) (Wolfheim, 1983; Fooden, 1976; Hill, 1974).

Ecological

Stumptail macaques are thought to occupy forests from the tropical broadleaf evergreen lowlands to the drier subtropical broadleaf uplands, ranging from sea level to 2500m (Eudey, 1984; Wolfheim, 1983; Hill, 1974; Bertrand, 1969; Fooden et al., 1985). It is also speculated that most of their time is spent foraging on the floors of these forests, dispersing to the trees only when alarmed (Hill, 1974).

The variety of their diet is virtually unknown, outside of what is taken during raids on crops [e.g., potatoes (McCann, 1933), rice (Bertrand, 1969)]. Field observations and posthumous examination of stomach contents suggest that the species is omnivorous (Bertrand, 1969; Fooden et al., 1985).

FIGURE 3.2. Geographic distribution of Macaca arctoides in Asia (adapted from Wolfheim, 1983).



Social

To quote Wolfheim (1983:465): "No estimates of population density or home range size could be located. Group sizes of 25 to 30 (McCann, 1933), up to 29 (9 troops; Bertrand, 1969), up to 50 (Medway, 1969), 5 to 50 (Fooden, 1971), and 14 to 15 (Fooden, 1976) have been reported." Only recently have the numbers of 20-30 individuals per group been suggested as normal based on brief contacts in the wild (Fooden et al., 1985).

PREVIOUS STUDIES OF SOCIAL BEHAVIOUR

Wild

Little is known about stumptail macaques in the wild, and this includes information on social behaviour. To date, Bertrand's (1969) study stands as the only field project to record behavioural information at length, although observations were done on a group in Thailand not technically wild; the troop had been captive for a year and had been released just nine months prior to the studies commencement. This group was observed intermittently for nine days and systematically for thirty-two days from 6 November 1965 to 26 February 1966 (Bertrand, 1969). Information by other researchers is minimal and based only on occasional sightings (Fooden et al., 1985; Biswas and Diengdoh, 1977).

Captive

Observation of stumptails in captivity is more extensive. In the late 1960's, Blurton Jones and Trollope (1968) did a general study of social behaviour. Since then, research has included studies ranging from socio-sexual behaviour and dominance to affiliation and communication

(e.g., Chevalier-Skolnikoff, 1974, 1975, 1976; Peffer-Smith, 1978; Bernstein, 1980; Chamove, 1982; Anderson, 1981; Nash, 1982; O'Keefee et al., 1983; Smith, 1984; Daniel, 1984; Nieuwenhuijsen et al., 1985; Murray et al., 1985; Estep, 1986; Rhine, 1986). Three projects have focused on sexual interference (Gouzoules, 1974; Niemeyer, 1980; Bruce, 1984), as outlined in the previous chapter.

STUDY SITE

Studies of both kinds, however, have not been without their problems. Simply, little is actually known about stumptails in the wild, and ecological validity in captivity is nonexistent. Since this project sought a combination of ecological validity and easy subject access and identification, plus subjects that readily display sexual interference, a free-ranging population of stumptail macaques was preferred. As already noted, stumptails are known for their high rate of sexual interference.

Location

Accordingly, the site selected for study was Tanaxpillo, a small tropical island in Mexico occupied by a single free-ranging group of stumptail macaques. The island is located in Lake Catemaco in the southeastern state of Veracruz (Figure 3.3). Its coordinates are 18°21'30" N latitude, 94°00'00" W longitude.

Lake Catemaco is situated at an approximate elevation of 300m above sea level and is encompassed by the San Martin Tuxtla mountain range (Figure 3.4). It is a natural lake formed by previous volcanic activity and measures 11 km E/W by 8 km N/S (Estrada, 1978). Five islands exist within the lake, four of which are located in the lake's north central corner. These

FIGURE 3.3. Geographic location of Tanaxpillo in Lake Catemaco, state of Veracruz, Mexico (adapted from Soto-Esparza, 1976).

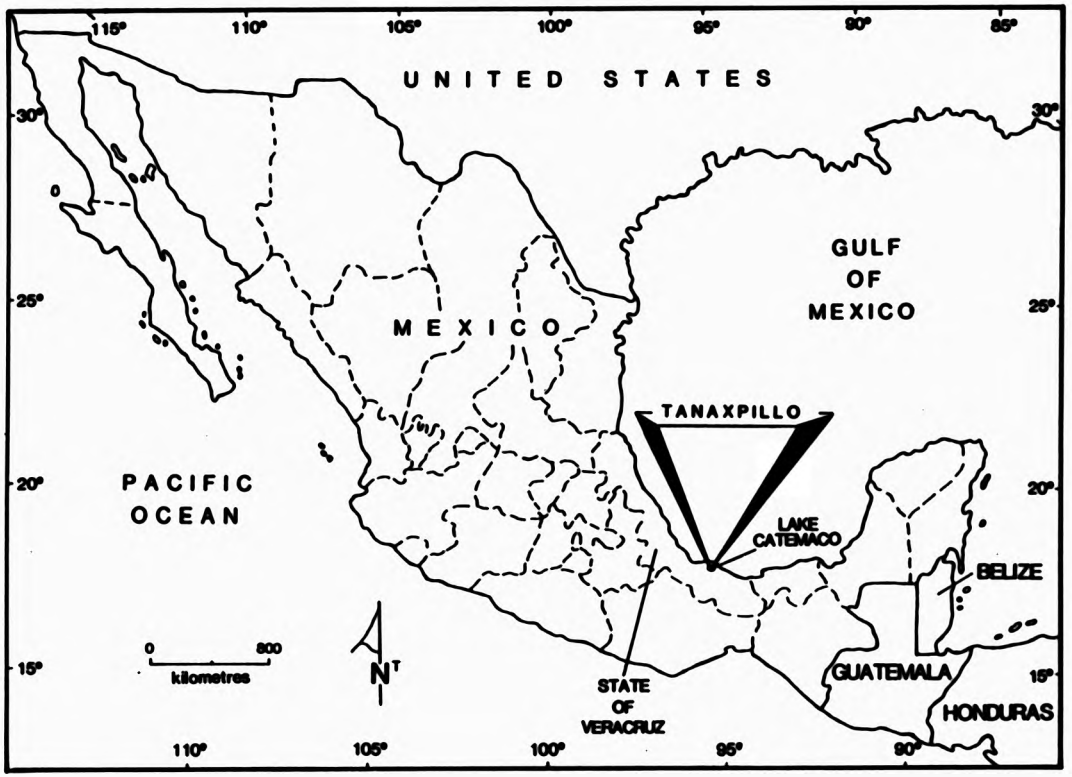
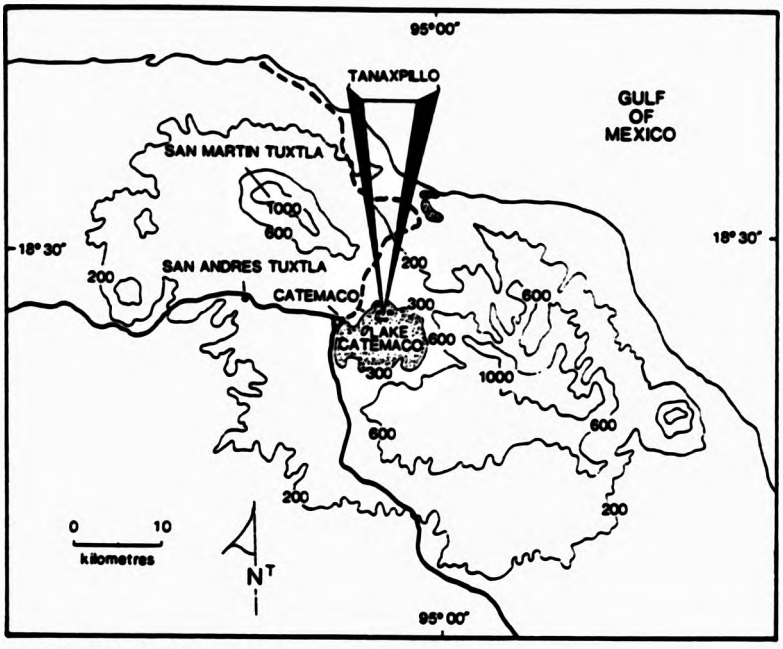
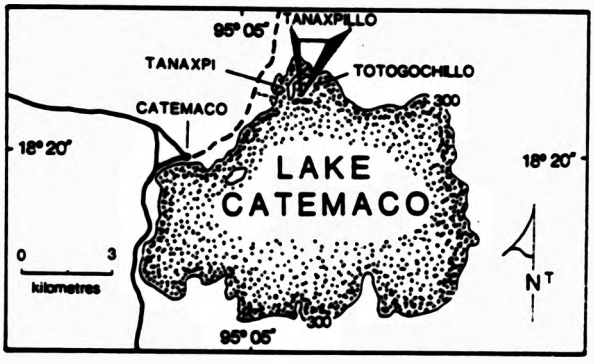


FIGURE 3.4. Elevations in the San Martin Tuxtla mountain range, Veracruz, Mexico (adapted from Soto-Esparza, 1976).



Elevations are in metres.

FIGURE 3.5 Location of Tanaxpillo within Lake Catemaco, Veracruz, Mexico (adapted from Lot-Helgueras, 1976).



include Tanaxpi, Totogochillo and the two islands which make up Tanaxpillo (Figure 3.5). The two study islands are just over .5 ha and are oriented from east to west. The larger of the two islands is to the east of the smaller. Figure 3.6 shows the exact orientations and dimensions of both.

Flora and Fauna

The vegetation on Tanaxpillo is secondary rain forest and consists of evergreen trees, vines, shrubs, grasses, cactus and water plants (Figures 3.7-3.12), and, overall, is probably not too different from the vegetation found in southeast Asia. The fauna includes iguanas, other lizards, frogs, snakes, mice, birds and insects. Although scientific names are not available, local vernacular names for the vegetation on the island of Totogochillo are partially listed in Estrada (1978). The vegetation on Tanaxpillo is similar, but of greater density.

Climate

The climate in the Catemaco area is tropical with a mean annual temperature of 24.1°c, again, not too unlike southeast Asia. The average high is 27.1°c occurring in May and the average low is 19.8°c occurring in January (Soto-Esparza, 1976).

The average yearly rainfall is 4935mm (Estrada and Estrada, 1976b). Most of this comes during the rainy season from June through September, but a portion falls during the winter months. Storms usually arrive from the north or northeast and are referred to locally as "Nortes".

Subject's History

On 15 August 1974 a group of 20 stumptail macaques were released on Totogochillo (Figure 3.5). These individuals were then followed by 12

FIGURE 3.6. Dimensions of Tanaxpillo within Lake Catemaco, Veracruz, Mexico (Barney-Guillermo, personal communication).

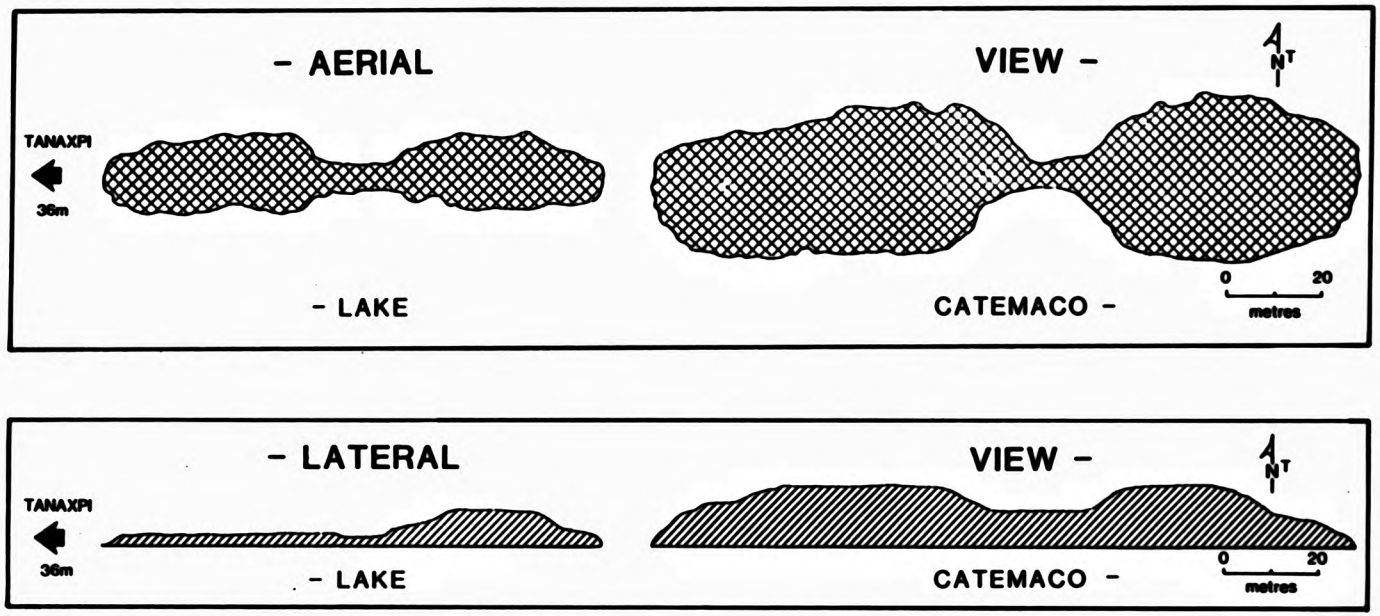


FIGURE 3.7. Tanaxpillo from a distance (photo centre) showing the Tuxtla range in the background. The vegetation is secondary rain forest.

FIGURE 3.8. The two portions of Tanaxpillo showing an outline of its canopy.

FIGURE 3.9. Another view of Tanaxpillo's canopy.

FIGURE 3.10. Partial view of Tanaxpillo looking southwest toward the town of Catemaco.

FIGURE 3.11. Partial view of Tanaxpillo looking west.

FIGURE 3.12. Partial view of Tanaxpillo looking east toward the more open area of the larger of the two islands.

more on 7 November 1974 for a total of 32 (Table 3.1) (Estrada, 1978; Estrada and Estrada, 1976b). Both groups had been part of a larger group (N=56) housed since 1971 in an outdoor enclosure at the Caribbean Primate Research Centre in Sabana Seca, Puerto Rico. Twelve of the individuals had been captured in the wild in Thailand. Twenty others were born in Puerto Rico (Table 3.1).

During their captivity at Sabana Seca, several of the individuals were used for a number of unknown years as experimental control subjects at the Rutgers University Medical School in New Brunswick, New Jersey (Estrada, 1978). McGregor was the only individual released on Totogochillo who was specifically known to have been a part of these experiments (Table 3.1). Others may have also been involved, but because of inadequate record keeping in both New Brunswick and Sabana Seca, this is uncertain. What is certain, however, is matrilineal descent (Estrada, 1978). An updated outline is presented in the following chapter.

A joint effort between the Universities of Mexico and Veracruz, the Behavioral Science Foundation, and Rutgers University Medical School was responsible for the group's initial transport and release (Estrada and Estrada, 1976b). On release, the primary responsibility fell to the University of Mexico who saw to its provisioning of corn and tropical fruit (e.g., Figures 3.13-3.15). This usually occurred daily, but sometimes every two to three days. It was supplemented by the natural vegetation that already existed on the island (e.g., Figure 3.16).

From the outset, the subjects were free-ranging and completely habituated to human observation (Estrada and Estrada, 1976b). They were also individually named and identified only by sight. Furthermore, the presence of boats with tourists arriving to view the group has continued from the time of release (Estrada and Estrada, personal communication;

TABLE 3.1. Composition of the two groups of stumptail macaques released on Totogochillo during August and November, 1974 (adapted from Estrada, 1978; Estrada and Estrada, 1976a, 1976b, 1981).

RELEASED 15 August 1974					RELEASED 7 November 1974				
Name	Sex	Birth (M/Y)	Age In Months (8/74)	Birth Place	Name	Sex	Birth (M/Y)	Age In Months (11/74)	Birth Place
Gordo	M	?	?	W	McGregor*	M	?	?	W
Negra	F	?	?	W	Carlos	M	?	?	W
Flor	F	?	?	W	Margarita	F	?	?	W
Roja	F	?	?	W	Flaca*	F	?	?	W
Jarocha*	F	?	?	W	Canela	F	?	?	W
Blondie*	F	?	?	W	Bunny	F	?	?	W
J.D.*	M	1/72	32	PR	Meme	M	2/73	22	PR
Chimuelo*	M	4/72	29	PR	Pablito	M	8/73	16	PR
Negrita	F	7/72	26	PR	Blanca*	F	3/74	9	PR
Nanche	F	7/72	26	PR	Elena*	F	4/74	8	PR
Jobo*	M	11/72	22	PR	Pierre*	F	7/74	5	PR
Chano	M	2/73	19	PR	D.J.	M	9/74	3	PR
Malita	F	3/73	18	PR					
Chica	F	7/73	14	PR					
Pancho*	M	7/73	14	PR					
Bonita	F	8/73	13	PR					
Amigo	M	9/73	12	PR					
Solita	F	11/73	10	PR					
Gallo	M	8/74	1	PR					
Rosy*	F	8/74	1	PR					

W= wild
PR= Puerto Rico
?= unknown
*= member of study group

FIGURE 3.15. Provision of corn.

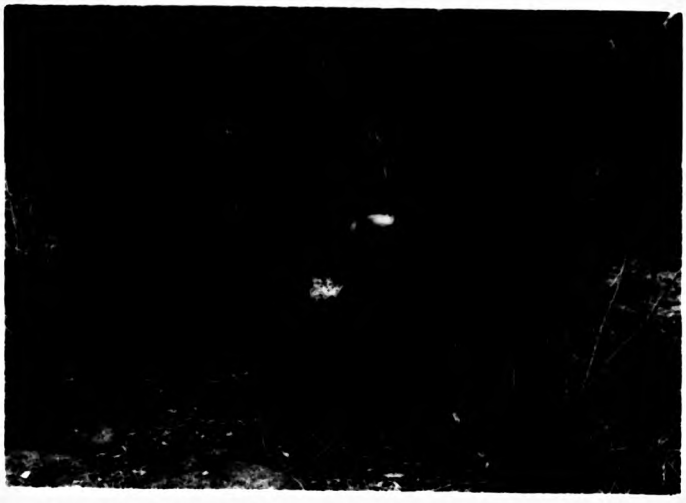


FIGURE 3.16. Supplemental feeding by stumptails on natural vegetation.

FIGURE 3.13. Provisioning of bananas.

FIGURE 3.14. Provision of bananas controlled by Pancho (centre right) and McGregor (centre left.

Caba-Vinagre et al., personal communication; personal observation) (Figures 3.17 and 3.18).

While on Totogochillo, Estrada and his colleagues (e.g., Estrada and Estrada, 1976b, 1977, 1978, 1981, 1984; Estrada et al., 1977; Estrada and Sandoval, 1977; Estrada, 1978; Estrada et al., 1978a, 1978b) carried out systematic studies of the group's ecology and behaviour. During this time, subjects were removed from the island only once. In February, 1976, five individuals were permanently removed to the Hospital of Neurology in Mexico City to be used in biomedical research (Estrada and Estrada, 1981, personal communication).

In June, 1979, the group was transferred to the slightly larger island of Tanaxpillo (Figure 3.5) (Rodriguez-Luna et al., 1982; Caba-Vinagre et al., personal communication). The purpose was to prevent overcrowding. Shortly thereafter, the responsibility for the group was transferred to the University of Veracruz, as was responsibility for continued research (e.g., Caba-Vinagre, 1984; Caba-Vinagre et al., 1986).

FIGURE 3.17. Arrival of a tourist boat to the island.

FIGURE 3.18. Stumptail/tourist interaction.

CHAPTER 4

METHODS

SUBJECTS

In November, 1983, the population on Tanaxpillo consisted of a single group of stumptail macaques composed of 54 individuals: 34 females and 20 males. Totals by subgroup of age and sex are listed in Table 4.1. As noted in the last chapter, this structure is similar to what is presently known about populations in the wild (Wolfheim, 1983).

During the study, four infants were born, three males and one female. One subadult female also died of unknown causes. These changes increased the groups's size to 57 by late May, 1984. The subadult female was included in the data, as were two of the infant males. The other infant male and the infant female were not because they were born just prior to completion of observation. Table 4.2 lists the group's composition by subject's name, sex, age-group, age in months, and month, year and place of birth. Figure 4.1 presents the group by matriline (Caba-Vinagre et al., unpublished birth records).

TABLE 4.1. Number of subjects on Tanaxpillo by subgroup of age and sex. Figures represent group composition from November, 1983 through May,1984.

SUBJECTS

Subgroup	Birth Year	Age In Months (5/84)	Male	Female
Adult	FB-'78	66- ?	7	16
Subadult	'79-'81	30-65	9	9*
Juvenile	'82-'82	18-29	3	4
Infant	'83-'84	0 -17	4@	6+
		Totals:	23	35

FB= feral born

*= one subadult female died during the study leaving the total number of individuals by late May, 1984 at 57 rather than 58, the sum of the above two columns

@= 3 males were born in mid to late May, 1984

+= 1 female was born in late May, 1984

?= unknown

TABLE 4.2. Group composition on Tanaxpillo by individual subject from November, 1983 through May, 1984.

FEMALES					MALES				
Name	Age Group	Birth (M/Y)	Age In Months (5/84)	Birth Place	Name	Age Group	Birth (M/Y)	Age In Months (5/84)	Birth Place
Blondie	A	?	?	F	McGregor	A	?	?	F
Flaca	A	?	?	F	J.D.	A	1/72	149	PR
Jarocha	A	?	?	F	Chimuelo	A	4/72	146	PR
Negra	A	7/72	143	PR	Jobo	A	11/72	139	PR
Blanca	A	3/74	123	PR	Pancho	A	7/73	131	PR
Elena	A	4/74	122	PR	Tigre	A	12/74	114	TT
Pierre	A	7/74	119	PR	Luciano	A	9/76	93	TT
Rosy	A	8/74	118	PR	Roberto	SA	3/79	63	TN
Bruja	A	10/74	116	TT	Santos	SA	4/79	62	TN
Lolita	A	3/77	87	TT	Bruno	SA	7/79	59	TN
Fanny	A	1/78	77	TT	Flan	SA	7/79	59	TN
Lucia	A	6/78	72	TT	Blair	SA	10/79	56	TN
Teresa	A	7/78	71	TT	Mario	SA	6/80	48	TN
Canela	A	7/78	71	TT	Wilfrido	SA	10/80	44	TN
Juanita	A	7/78	71	TT	Lorenzo	SA	5/81	37	TN
Mirna	A	11/78	67	TT	Bruto	SA	6/81	36	TN
Flossie	SA	7/79	59	TN	Blas	J	4/82	26	TN
Martha+	SA	12/79	54	TN	Florencio	J	5/82	25	TN
Miriam*	SA	12/79	54	TN	Miguelito	J	5/82	25	TN
Ucilia	SA	5/80	49	TN	Teo	I	10/83	8	TN
Sigri	SA	9/80	45	TN	Millo@	I	2/84	4	TN
Enriqueta	SA	10/80	44	TN	Martin@	I	4/84	2	TN
Marcela	SA	5/81	37	TN	Ernesto@	I	5/84	1	TN
Flavia	SA	6/81	36	TN					
Blasita	SA	9/81	33	TN					
Piedad	J	3/82	27	TN					
Rosa	J	4/82	26	TN					
Brisa	J	6/82	24	TN					
Elpidia	J	11/82	19	TN					
Lupita	I	3/83	15	TN					
Florinda	I	4/83	14	TN					
Lourdes	I	6/83	12	TN					
Blonny	I	10/83	8	TN					
Blenda	I	10/83	8	TN					
Julieta@	I	5/84	1	TN					

A= adult SA= subadult J= juvenile I= infant
F= feral PR= Puerto Rico TT= Totogochillo TN= Tanaxpillo
*= died during study
@= born during study
?= unknown
+= gave birth as a subadult

FIGURE 4.1. Group composition on Tanaxpillo by matriline from November, 1983 through May, 1984. Presented in descending order according to overall dominance.

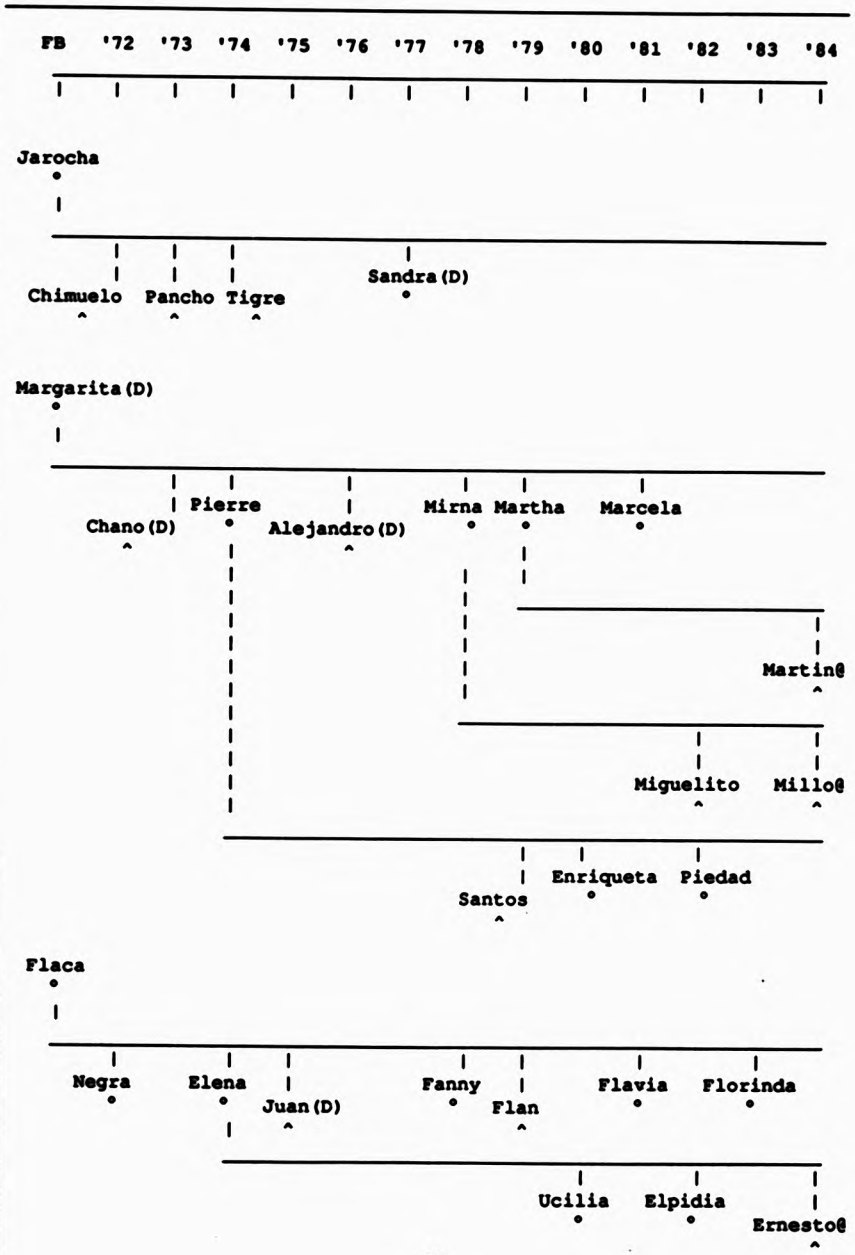


FIGURE 4.1. Continued.

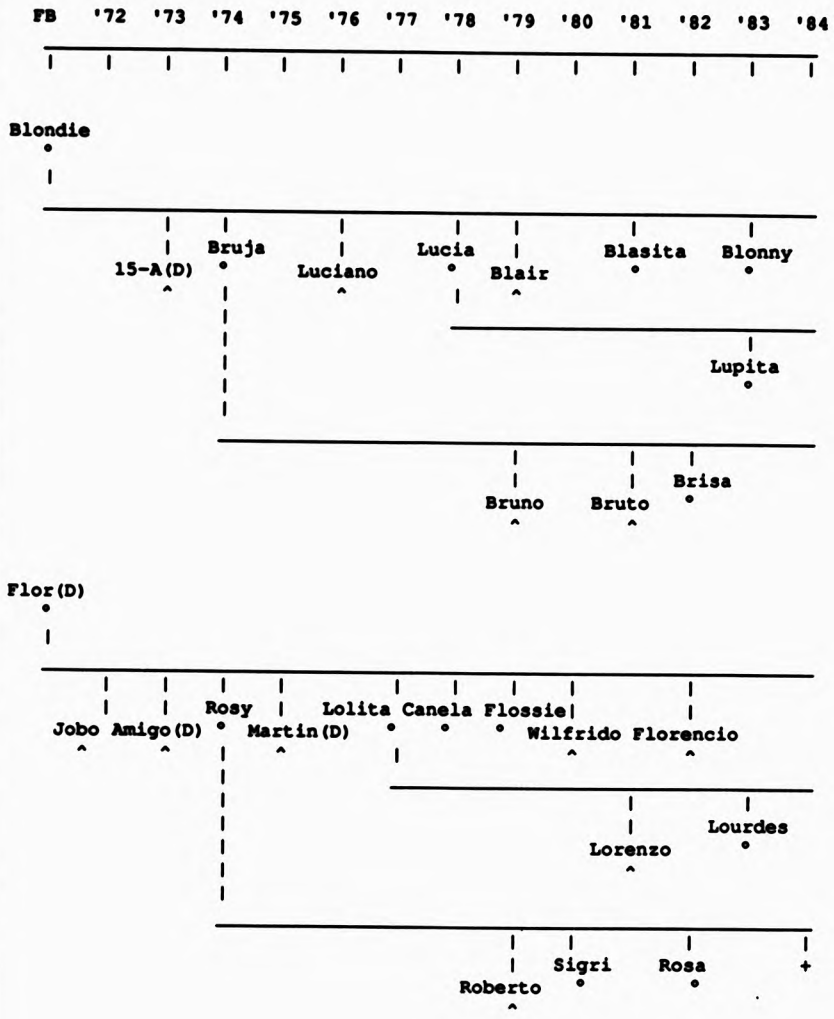
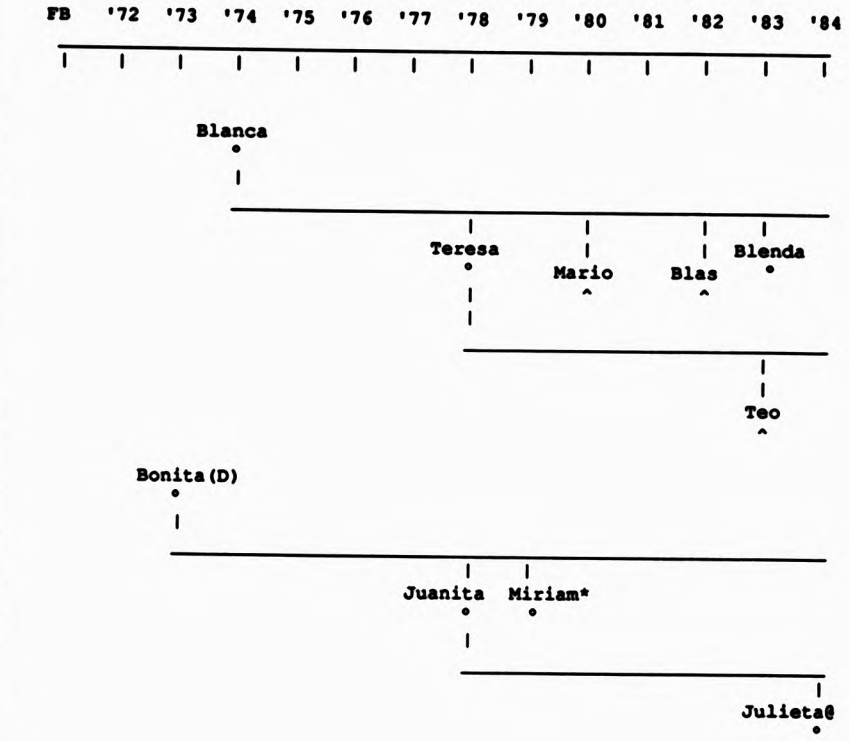


FIGURE 4.1. Continued.



FB= feral born '72-'84= year of birth °= female ^= male

(D)= died before study *= died during the study @= born during study

+= breech birth ?= unknown matriline

APPARATUS

The apparatus used included a Casio chronometer, a Sony portable cassette recorder, Zeiss Icon 7x50 binoculars, a Zeiss Icon camera with 55mm lens, a 22x40 cm clip board, and copies of seven types of check-sheets. The check-sheets were designed to meet the study's specific criteria. Each was based on guidelines set by Hinde (1973). Four were used daily in the field. The other three were filled in from transcriptions of cassette recordings of mating behaviour after returning from the field. The recordings were made by sampling the monkey's spontaneous behaviour. More will be said below about each of the sampling regimes. All observations were made on foot with the observer moving freely amongst the subjects without visible disturbance.

PROCEDURES

The study lasted from 20 November 1983 to 19 May 1984. By the end, contact with the subjects totalled 600 hours, and these were dispersed over 83 days. Table 4.3 gives hourly totals by day and month. Starting and finishing times are also included, as are total numbers of matings and numbers with sexual interference. The time it took to learn the identity of the subjects on sight is not included.

On days that observations occurred (Table 4.3), my stay on the island averaged 7.2 hours (range=1-10). Most of days began with arrival at about 7:45 to 8:00 am. This was preceded by a 5 km walk or occasional bus ride, followed by a 1 km boat row. Departure was usually between 3:45 and 4:00 pm. The earliest time of arrival was 7:00 am and the latest departure 6:30 pm (see Table 4.3 for the exact times). I tried to divide the 8-hour

TABLE 4.3. Observation hours by day and month from 20 November 1983 through 19 May 1984. [Figures to the left of the hourly total represent respective arrival (at top) and departure (at bottom) times. Figures to the right represent matings seen (top) and matings receiving sexual interference (bottom).]

Day	NOV '83	DEC '83	JAN '84	FEB '84	MAR '84	APR '84	MAY '84
1				7:50 (8) 15:50	7:30 1 (8) 15:30 1	7:15 (8) 15:15	9:30 (4) 13:30
2			7:55 (7) 14:55	7:50 1 (8) 15:50 0	7:25 (5) 12:25	7:15 (8) 15:15	7:15 (10) 17:15
3			7:50 (8) 15:50	7:35 (8) 15:35		7:10 (8) 15:10	7:25 (10) 17:25
4			8:40 2 (8) 16:40 2	7:50 4 (8) 15:50 3		7:15 (6) 13:15	7:20 (10) 17:20
5			12:00 1 (5) 17:00 0			9:45 (2) 11:45	8:30 (6) 14:30
6				7:50 11 (8) 15:50 11	7:35 (8) 15:35	7:10 (6) 13:10	
7			8:10 (9) 17:10	7:45 (8) 15:45			
8			1:00 (4) 17:00	7:45 (8) 15:45			
9			7:55 (8) 15:55	7:50 (8) 15:50		7:05 (8) 15:05	
10			8:00 (4) 12:00	7:50 4 (8) 15:50 4			
11			8:00 (4) 12:00	7:45 (5) 12:45	7:15 (10) 17:15	9:00 (4) 13:00	
12			7:55 (8) 15:55		7:15 (10) 17:15	7:00 (8) 15:10	

TABLE 4.3. Continued.

Day	NOV '83	DEC '83	JAN '84	FEB '84	MAR '84	APR '84	MAY '84
13			7:50 5 (8) 15:50 5	1:45 2 (3) 16:45 1	7:20 (7) 14:20		
14			7:40 (8) 15:40	7:45 (8) 15:45	7:10 1 (8) 15:10 1		
15				7:50 7 (8) 15:50 7			
16			7:50 (8) 15:50	7:50 9 (8) 15:50 2			
17			7:55 2 (8) 15:55 2	7:45 4 (8) 15:45 3			
18			7:50 (8) 15:50				
19			7:55 1 (8) 15:55 0			7:00 (6) 13:00	Departed Mexico
20	Arrived in Mexico		7:50 3 (8) 15:50 3	7:45 1 (8) 15:45 1	11:30 4 (7) 18:30 4	8:05 (4) 12:05	
21		8:30 (6) 14:30		7:40 2 (8) 15:40 2	7:15 1 (10) 17:15 1		
22		8:20 3 (6) 14:20 3		7:50 (8) 15:50	7:20 (10) 17:20		
23		8:30 (4) 12:30	7:50 (8) 15:50	7:50 (8) 15:50			
24			7:55 2 (8) 15:55 1	7:30 (8) 15:30			
25			7:45 14 (10) 17:45 14	7:15 (7) 14:15			

TABLE 4.3. Continued.

Day	NOV '83	DEC '83	JAN '84	FEB '84	MAR '84	APR '84	MAY '84
26		8:40 (7) 15:40	7:50 (8) 15:50				
27		8:30 1 (4) 12:30 0	7:15 (9) 16:15	7:25 (5) 12:25			
28		8:40 (5) 13:40		7:15 (8) 15:15	7:20 1 (6) 13:20 0		
29				7:25 13 (7) 15:25 12			
30		8:25 (4) 12:25			7:10 (8) 15:10		
31			7:50 1 (8) 15:50 0		7:40 12 (8) 15:40 12		
Totals:		(36)	(172)	(179)	(105)	(68)	(40)
Matings/Interf.:		4/2	31/27	58/46	20/19	0/0	0/0

TOTAL FIELD DAYS: 83

TOTAL FIELD HOURS: 600

MEAN HOURS PER DAY: 7.2

sampling day into two halves: 4 hours in the morning and 4 hours in the afternoon. These times were altered mainly by foul weather and mating sequences between subjects. The actual sampling days were determined by logistics (e.g., the avoidance of tourists).

Sampling

Sexual interference was of primary interest, and, by chosen definition, it occurred only during matings. Therefore, all observed matings were recorded in detail, as were all observed instances of interference and retaliation (see Table 4.4 for definitions of behavioural categories).

Because of its potential effect on predicting who may interfere, samples on affiliation were also collected. Samples on dominance were recorded for the same reason (see Table 4.4).

The remaining two categories of data collected were oestrus and *ad libitum:* the former for a predictor of forthcoming matings, and the latter to note any behaviour of interest not already included under the previously selected categories (Table 4.4). Portions of the *ad libitum* data proved very informative and provide the framework for Chapter 9. The samples on oestrus, however, were of little value and did not reliably predict impending matings. The lack of noticeable swelling of female perineum in stumptails, or other signs of oestrus, for that matter, is well documented (Murray et al., 1985; Butler, 1974; Hafez, 1971; Napier and Napier, 1967). The only reliable predictor was previous mating.

Protocols

Sampling regimes were based on Altmann (1974).

After arriving on the island each day, if no matings were in progress, I began by taking samples of affiliation. Affiliation was given sampling

TABLE 4.4. Definitions of behavioural categories sampled. See Appendix for terms and definitions of behaviour that can occur in each category. The category of *ad libitum* is not listed in the Appendix because it is open ended. Also, the subcategory of *response behaviour* is included within the category of *retaliation*.

CATEGORY/SUBCATEGORY*	DEFINITION
Mating	Entry of female genital canal by male penis followed by pelvic thrusting to ejaculation. May be accompanied by withdrawal of no more than 60 seconds before reentry preejaculation. Terminates with postejaculatory genitalia separation.
Sexual interference	Orientation toward a mating pair recognised by staring and approaching by at least one step measured from the earliest moment of ejaculation to the end of the tie.
Retaliation	Agonism by either or both of the mating pair in response to sexual interference.
Response Behaviour	Behavioural reaction of intruder(s) to retaliation.
Affiliation	Non-agonistic interaction between individuals.
Dominance	Dyadic agonistic interaction involving aggression by the actor and submission by the recipient.
Oestrus	Female sexual receptivity.
Ad Libitum	Selected behavioural patterns of projected importance not already included in the above categories.

* Data on ***mating***, ***sexual interference***, and ***retaliation*** were collected by using a combination of *focal-animal* and *one-zero sampling*; *focal-animal sampling* served for collecting data on ***affiliation***, and ***dominance*** and ***oestrus*** data were collected through *sampling all occurrences of some behaviour* [see text (protocols) for definitions of methods].

priority because of its potential effect on sexual interference. Each sample lasted for 10 minutes and was conducted through *focal-animal sampling;* defined here as observing one individual for a specified time and recording several predetermined kinds of his or her social behaviour. The identities of the focal animal's partners and the durations and frequencies of their specific interactions are recorded. This method was chosen because durations and frequencies of affiliative behaviour are best sampled in a focal manner. The subjects tested included 16 adult and 3 subadult females, and 7 adult and 5 subadult males. The subadults, both male and female, were born in 1979 and were of a minimum age of 47 months at the beginning of the study. These subjects were chosen because they were the most likely to be involved in subsequent mating.

During observation, a list of these subjects was taped to the inside base of the clip board, females followed by males. As long as there were no boats with tourists immediately present, each was addressed in turn. Tourists often fed the subjects, altering their behaviour. If, at the end of one sample, the next individual on the list could not be found within 5 minutes, it was passed over and sampled at the next available opportunity. This procedure continued until each individual on the list was observed, then the entire process was repeated.

By the end of the study, 820 10-minute samples were collected for a total of 136 hours and 40 minutes. Each subject was sampled 26 times (4 hours and 20 minutes). The behaviour and definitions used in judging affiliation are listed in the Appendix.

While focal samples of affiliation were being done, or in between such samples, data on dominance and oestrus were recorded opportunistically. This was done simply and quickly, without effecting other procedures. For dominance, when one or more act(s) of aggression were displayed by one

individual toward another, resulting in one or more act(s) of submission by the latter, the behaviour (see Appendix) involved and the time of day were logged on the dominance check-sheet. After one recording, if the same two individuals happened to be involved in the another episode of dominance, two separate bouts were recorded if the individuals' interactions were separated by an interval of at least 5 seconds. Similarly, signs of and behaviour reflecting oestrus were recorded on its respective check-sheet (see Appendix). The method use for both categories was *sampling all occurrences of some behaviour* . This method is defined as observing and recording each occurrence of particular predetermined behaviour, along with the identities of the individuals involved. It was the method chosen for dominance and oestrus because it make it possible to collect data simply and quickly on several categories simultaneously.

The same sampling method, approach and rational were used in recording *ad libitum* information. The data collected, however, were wide-ranging and guided only by my guess as to what was important. All categories of behaviour not already being systematically sampled were considered (e.g., occurrences of behaviour not previously regarded as "normal"). This led to 100 pages of transcription at the end of the study.

For sampling mating, sexual interference, and retaliation, *focal-animal sampling* was implemented, in combination with *one-zero sampling*, which is defined here as simply recording the presence or absence of predetermined behaviour over the course of a mating (Table 4.4). For example, if a particular behaviour occurred three times during a mating sequence, a score of one would be recorded. These two methods were used together for quickness and accuracy of recording. When mating occurred, the collection of all other data was abandoned and attention was shifted immediately to the mating. A hand-held portable cassette recorder was then

used to note the pair's identity and a one-zero frequency of their behaviour (listed in the Appendix). Most of the matings received sexual interference, along with some form of retaliation (see Appendix), and these data were also recorded using the same method. The abandoned data was eventually discarded and sampling was begun anew after the mating or series of matings had come to an end. This was because mating and its associated behavior were of primary research interest.

Ultimately, 6 hours of tape transcribed to 113 pages and included data on 113 matings, 94 of which experienced sexual interference. These data were then placed on their respective check-sheets after returning from the field.

ANALYSIS

Measures

To assess the differences in sexual interference by different individuals, it was thought desirable to have a single scale. To do this, using either frequency (e.g., total number of matings interfered with) or duration (e.g., total number of seconds spent in interference) for each subject was preferred. When implemented, however, linearly ranked subjects ended up with identical scores making it impossible to distinguish between them. Simple frequency and duration also revealed very little as to the intensity of interference. A more precise measure was, therefore, required.

To meet this requirement, a third measure, frequency of behaviour, or total one-zero sexual interference behaviour (I), plus total one-zero retaliatory (R) and response behaviour (RB), was multiplied by the total duration of interference (D) for each subject. Put simply, a combined score (CS) was formed:

$$CS = D(I + R + RB)$$

As stated above, other behavioural measures, like frequency and duration, had a number of tied rankings. For example, frequency had 9 ties involving 35 individuals, duration had 2 ties involving 4, and behaviour had 7 involving 15. But when I+R+RB was multiplied by D, only 1 tied score involving 2 individuals was produced. (The total number of subjects interfering was 47.) Because of this, and in that each of the four measures were all highly correlated (Kendall coefficient of concordance, x^2=61.66, $p<.001$), the combined measure was the scale chosen to represent sexual interference throughout data analysis and in later chapters. Frequency of behaviour (I+R+RB) was also highly correlated with duration (D) [Spearman rank correlation coefficient test, r_s=.912, $p<.001$], and high degree of relatedness between measures demonstrates high intra-observer reliability (Martin and Bateson, 1986). Furthermore, it should be noted that an alternative way of calculating CS would be to add I+R+RB with D, but this calculation was not done because, like frequency and duration, it would not adequately reveal differences between individuals. Other methods of calculating CS were not used for the same reason [e.g., D (I+R), D (I)]. Also, even though it was behaviour performed by individuals other than intruders, the reason that retaliatory behaviour (R) was used in the CS calculation was because it appeared equally important compared with the three other measures (I, RB and D) in measuring the intensity of interference. For example, if a mating male retaliated against an intruder, his behaviour seemed to directly effect the intruder's interference and response behaviour and duration of interference. Therefore, since these measures were most likely interrelated, it was important to use all four in

calculating an accurate overall score of interference for each intruder.

Finally, to test if the amount of data used in analysis were sufficient to detect real effects, because of its importance in latter discussion, a Spearman rank correlation coefficient test was performed on tie durations (see Chapter 6) to see if they correlate in the 113 matings when split into two equal halves. This method is known as *split-half analysis* (Martin and Bateson, 1986) and compares the ranks of the two groups. Its function is to measure the degree of association between two sets of like data when treated separately. Since they did correlate (r_s=.366, p=.010), it is generally assumed that the results presented in later chapters are based on an adequate amount of field information. Also, when a Mann-Whitney U test is calculated on the same two sets of data to determine if they were significantly different, it was found that they were not (z=-1.033, p=.302). This increases the likelihood that the data collected are sufficient to provide the statistical power required for testing later hypotheses.

Statistics

The statistics in the study were calculated by computer using SPSS^x (SPSS Inc., 1986). Their use was guided by Siegel (1956), and each test is two-tailed. Levels of significance are at .05, .01, or as specified.

CHAPTER 5

THEORETICAL FUNDAMENTALS OF SEXUAL SELECTION AND SOCIOBIOLOGY

The aim of this chapter is to review briefly the elementary fundamentals of sexual selection and sociobiological theory upon which discussions in later chapters are based. Central to both is Charles Darwin's (1859) view that organic evolution is a fact and it is occurring through the process of natural selection; synthesised in modern biology to mean differential genotypic reproduction among conspecifics (Daly and Wilson, 1978). The present study's approach is, therefore, ultimately functionalist, concerned with how social behaviour serves an individual's reproductive fitness, and individually selectionist, rather than selectionist by group or species. Individuals biologically reproduce; groups and species do not.

SEXUAL SELECTION

Darwin (1871) coined the term sexual selection to explain the processes responsible for the sexual differences he observed in appearance and behaviour between males and females of the same species. Although, at the

time, he believed sexual selection to be a process separate from natural selection, that is, mating success as opposed to success in survival, it is now generally accepted that the former is only one aspect of the later since both rely on differential reproduction of individuals and their genes. In other words, sexual selection is but a single area where natural selection proceeds (Barash, 1982).

Wilson (1975: 595) defines sexual selection as "the differential ability of individuals of different genetic types to acquire mates." Because of the differences in cost between the sexes in both gamate production (Richards, 1927; Bateman, 1948) and parental investment (Trivers, 1972), it is theorised that males generally compete amongst themselves for mating access to females, which is intrasexual selection, while females chose with which of the males to mate, which is intersexual selection. In nature, both processes are no doubt complementary and operate simultaneously (Hausfater, 1975; Krebs and Davies, 1978).

Intrasexual selection can occur overtly, and also in ways less obvious. Outright fighting between males is one of several overt examples. Less distinguishable examples are individuals interfering with other's matings (which is the concern of the this study) and varying abilities among males to search out or court prospective females (Krebs and Davies, 1984). These characteristics presumably evolve because the benefits produced outweigh the costs incurred, measured in terms of reproductive success.

The process of intersexual selection is more difficult to identify. Its existence, however, is undeniable, for example, the extreme and complex patterns of species-specific courtships (Krebs and Davies, 1984). A more specific example of intersexual selection is female rejection of courting male advances by actively protesting and preventing mating (for primate review see Smuts, 1987; Cox and Le Boeuf, 1977; Cox 1981). As with

intrasexual selection, these behaviours have presumably evolved because of their reproductive advantages.

Sexual selection, however, is more than just conservatively viewed theory (Hrdy and Williams, 1983; Wasser and Waterhouse, 1983; Hrdy, 1984). Researchers are beginning to recognise great variation in strategy among individuals within each sex. Instances where females compete for mates, common among males, and males choose, reminiscent of females, have both been recorded (e.g., Wasser, 1983; Packer, 1979). Again, measurement is in terms of reproductive fitness. Sexual selection may, therefore, not be quite as limiting as originally proposed. Table 5.1 lists sexual selection's various forms.

SOCIOBIOLOGY

With both sexual and natural selection as its foundation, sociobiology has within the last decade revolutionised the scientific study of social behaviour. Not surprisingly, then, sociobiology is theory upon which this study is based.

As defined by Wilson (1975: 595), sociobiology is "the systematic study of the biological bases of all social behaviour." It differs from earlier biological efforts in three fundamental ways: its dependence on individual selection, its view of individuals as reproductive strategists, and its use of inclusive fitness theory (Daly and Wilson, 1978).

As mentioned earlier, individuals reproduce, and not groups or species. Individuals are also strategists when viewed reproductively over time. Inclusive fitness builds on this and includes an individual's biological relatives (Hamilton, 1964a and b). Hrdy and Williams (1983:4) define inclusive fitness as "the sum of an individual's own behaviour plus the

TABLE 5.1. The varieties of sexual selection (adapted from Wilson, 1975).*

I. Intersexual Selection

- A. Mate Choice
- B. Optimal Timing of Mating

II. Intrasexual Selection

- A. Competition: Premating
  1. Mate Finding
  2. Territorial Exclusion
  3. Intergroup Dominance
  4. Dominance For Mate Access
  5. Temporary Absence From Group Of Courting Pair
- B. Competition: Postmating
  1. Sperm Displacement
  2. Induced Abortion Followed By Insemination (Bruce Effect)
  3. Infanticide Followed By Insemination
  4. Mating Plugs/Repellents
  5. Prolonged Mating
  6. Mate Defense

---

* May not be limited to one sex.

effect that his or her behaviour has on the fitness of relatives." Figure 5.1 diagrams the genetic relations between individuals within a hypothetical lineage. Table 5.2 provides the actual relationship coefficients between relatives. Overall, sociobiology considers all social behaviour to be a product of selection and, therefore, ultimately functional. Proximate causes are viewed only as mechanisms for achieving ultimate goals (Daly and Wilson, 1978).

To be classified as social, behaviour requires an interaction between at least two individuals. When this interaction occurs, sociobiology considers how the behaviour of the actor affects the relative costs and benefits in reproductive fitness of both itself and the recipient.

All social behaviours can be placed in one of four categories of social traits. These are altruistic, cooperative, selfish, and spiteful (Trivers, 1985). Each is determined by the way in which the reproductive costs and benefits are distributed between the actor and recipient. Their definitions and symbolic representation in costs and benefits in reproductive fitness are listed in Table 5.3.

A subcategory of spiteful traits, and the specific hypothesis addressed in this study, is *return-benefit spite*. Spite of this kind is defined as a social trait that is both immediately spiteful and ultimately selfish (Table 5.3). It is classified as spite because the actor's return benefit cannot often be directly witnessed or guaranteed. When it can, the trait may then be considered selfish. This proposal will be discussed in more detail in Chapters 8 and 9. But next, Chapters 6 and 7 respectively will present data collected on socio-sexual behaviour and sexual interference in stumptail macaques, and where appropriate, data on their affiliation and dominance. Behavioural data from other studies across species will also be summarized and compared, and the differences in findings will be discussed.

FIGURE 5.1. A hypothetical lineage demonstrating the genetic relationship between an individual *(self)* and his or her various relatives (adapted from Dunbar, 1987).

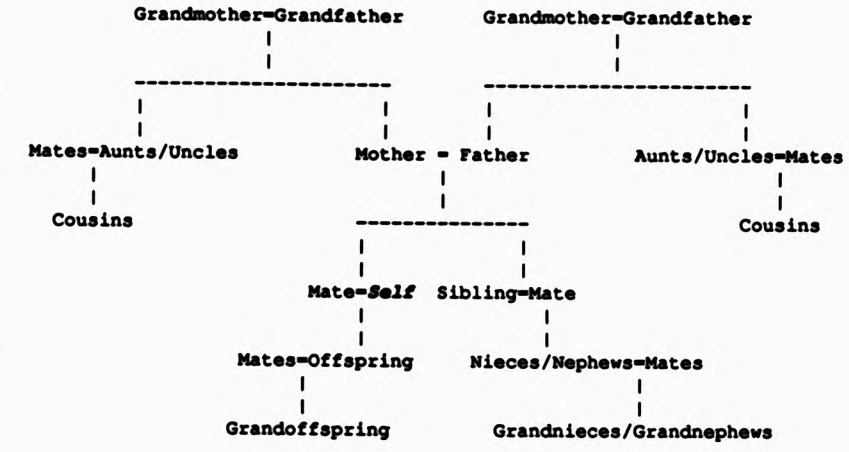


TABLE 5.2. Coefficients of relatedness between an individual *(self)* and a sample of his or her various relatives according to whether one or both parents are shared (adapted from Dunbar, 1987).

RELATIONSHIP TO *SELF*	RELATIONSHIP COEFFICIENT (r) (Same Mother/Father) Yes	No
Parents, Offspring	0.500	0.500
Siblings	0.500	0.250
Aunts/Uncles, Nieces/Nephews	0.250	0.125
Cousins	0.125	0.063
Grandparents, Grandoffspring	0.250	0.250
Identical Twin	1.000	---

(r)=1.000 (total genetic relationship, e.g., *self*, identical twin); less than total relationship is calculated by halving r each time a reproductive event separates *self* from the relation in question, halving the result if either the mother or father is not the same (excluding grandparents and grandoffspring)

TABLE 5.3. Definitions of social traits and symbolic representation of their costs and benefits in reproductive fitness (adapted from Trivers, 1985).

TRAIT/SUBTRAIT	DEFINITION	COST/BENEFIT Actor	Recipient
Altruistic	Behaviour that provides a benefit to the recipient at a cost to the actor.	-	+
Cooperative	Behaviour that provides a benefit to both the actor and recipient.	+	+
Selfish	Behaviour that provides a benefit to the actor at a cost to the recipient.	+	-
Spiteful	Behaviour that imposes a cost on both the actor and recipient.	-	-
Return-Benefit Spite	Behaviour that imposes an immediate cost on both the actor and recipient, but may ultimately contribute to a benefit for the actor.	-(+)	-

- = Cost
+ = Benefit

CHAPTER 6

SOCIO-SEXUAL BEHAVIOUR

To better understand stumptail macaque socio-sexual behaviour, and for later reference, a short review of the socio-sexual behaviour of the genus *Macaca* will begin this chapter. This will be followed by a brief description of stumptail mating, as well as brief descriptions of their unique post-ejaculatory phase referred to as the copulatory tie (Lemmon and Oakes, 1967) and their specialised genitalia morphology. The results on mating from this study will then be presented, followed by comparisons with and discussion of similar research. The purpose of the chapter is to provide information for theoretical discussion in both Chapters 8 and 9.

MACACA REVIEW

According to Fooden (1980), the genus *Macaca* can be subdivided into four species groups: the *M. silenus-sylvanus* group, the *M. fascicularis* group, the *M. sinica* group, and the *M. arctoides* group. These groups and their respective species are listed in Table 3.1. Since they appear to reflect the phylogenetic relationship among macaques (Melnick and Kidd, 1985), they will be used to structure the following outline. Where information is available, 11 basic attributes of socio-sexuality will be addressed for each species, or for the group as a whole. These include the

type of mating system present, solicitation behaviour of the male or female, whether the male copulation pattern reflects single or multiple mounts to ejaculation, ejaculation frequency, duration of consortships, and whether breeding and birth seasons exist. Also reviewed are whether females show external signs of oestrus, the length of a female's menstrual cycle, females' gestation length, interbirth intervals, and, finally, female age at first giving birth (see Table 6.1 for a summary).

M. Silenus-Sylvanus Group

Social Attributes

As noted in Table 3.1, the species included within this subdivision are the liontail, Moor, pigtail, Booted, Crested, Tonkean, and Barbary macaques. For each of these species, except for the Moor and Booted, mating systems are multimale (Melnick and Pearl, 1987; Hrdy and Whitten, 1987). Group structures of wild Moor and Booted macaques are virtually unknown, but they too probably contain more than a single adult male.

Initiation of matings among the species of this group is typically performed by both males and females (Hrdy and Whitten, 1987). Female solicitations range from the minimum of hindquarter presentation in most of the species to grabbing and jerking the males head in Barbary macaques. Male solicitations, on the other hand, usually involve touching the female's hindquarters and attempting to mount.

Male members of this group as a whole are considered by Fooden (1980) to be multiple-mount ejaculators (MME). In other words, copulations normally occur in a series of about 10 individual mounts before the male reaches ejaculation. However, this appears to be true for only the liontail, pigtail and Crested species (Sugiyama, 1968; Nadler and

TABLE 6.1. Attribute summary of *Macaca* socio-sexuality.*

	SOCIAL						SEXUAL					
Species (Vernacular)	Mating System	Solicitation Behaviour	Copulation Pattern	Ejaculation Frequency	Consortship Duration	Breeding/Birth Seasonality	Sex Skin (Oestrous)	Cycle Length (Days)	Gestation Length (Days)	Interbirth Interval (Months)	Age at First Giving Birth (Months)	Source
M. *Silenus-Sylvanus* Group (Fooden, 1969)												
Lion-tail	Multimale	Male: Touches hindquarters, attempts to mount, Female: Presents hindquarters	MME	-	Hours to days(?)	Non-Seasonal	Prominent swelling and reddening of the perineum	48	171.0	-	-	Hrdy and Whitten, 1987; Fooden, 1969; Sugiyama, 1988; Smith, 1984; Andelman, 1986; Dixson, 1983, Vancatova et al., 1986
Moor	Multimale(?)	Male: Touches hindquarters, attempts to mount(?), Female: Presents hindquarters(?)	MME(?)	-	Hours to days(?)	-	Swelling and reddening of the perineum	-	163	-	-	Melnick and Pearl, 1987; Fooden, 1969; Dixson, 1983, Harvey and Clutton-Brock, 1985
Pig-tail	Multimale	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters	MME	1.4/hr	Hours to 10 days	Non-Seasonal	Prominent swelling and reddening of the perineum	32	170	13.5	47.3	Hrdy and Whitten, 1987, Fooden, 1969, Hadler and Rosenblum, 1973, Chevalier-Skolnikoff, 1975; Smith, 1984; Andelman, 1986, Dixson, 1983, Melnick and Pearl, 1987; Harvey and Clutton-Brock, 1985
Booted	Multimale(?)	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters	MME(?)	-	Hours to days(?)	-	Swelling and reddening of the perineum	-	-	-	-	Melnick and Pearl, 1987, Fooden, 1969; Dixson, 1983
Crested	Multimale(?)	Male: Touches hindquarters, attempts to mount(?), Female: Presents hindquarters(?)	MME	-	Hours to days(?)	Non-Seasonal	Prominent swelling and reddening of the perineum	34	176	18	66	Melnick and Pearl, 1987, Dixson, 1977, 1983, Smith, 1984; Hrdy and Whitten, 1987; Harvey and Clutton-Brock, 1985, Hadshan and Bernstein, 1979
Tochaea	Multimale(?)	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters(?)	MME(?)	-	Hours to days(?)	-	Swelling and reddening of the perineum	-	-	-	-	Melnick and Pearl, 1987, Fooden, 1969, Dixson, 1983

TABLE 6.1. Continued

	SOCIAL						SEXUAL					
Species (Vernacular)	Mating System	Solicitation Behaviour	Copulation Pattern	Ejaculation Frequency	Consortship Duration	Breeding/Birth Seasonality	Sex Skin (Dectrous)	Cycle Length (Days)	Gestation Length (Days)	Inter-birth Interval (Months)	Age at First Giving Birth (Months)	Source
Barbary	Multimale	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters, grabs and jerks male's head	SME	-	1-93 minutes	Seasonal	Prominent swelling and reddening of the perineum	31	-	14.39 (31.5)@	48	Hrdy and Whitten, 1987; Took, 1986; Smith, 1984; Andelman, 1986; Dixson, 1983; Burton and Savchuk, 1982; Harvey and Clutton-Brock, 1985
M. fascicularis Group, Fooden, 1988												
Crabeating	Multimale	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters	MME/ SME	.66-1.33/hr	Hours to more than a week	Seasonal/ Non Seasonal	Perineal swelling and reddening decreases with age	31	162	13	46.3	Hrdy and Whitten, 1987; Malnick and Pearl, 1987; Shively, 1982; Caldecott, 1986; Smith, 1984; Harvey and Clutton-Brock, 1985
Japanese	Multimale	Male: Presents, touches hindquarters, "sexual attack"; Female: Presents hindquarters, mounts male	MME	.58/day	Hours to days	Seasonal	Perineal swelling and reddening increases with age	28	173	-	60	Hrdy and Whitten, 1987; Malnick and Pearl, 1987; Fooden, 1980; Shively et al., 1982; Smith, 1984; Andelman, 1986; Harvey and Clutton-Brock, 1985;
Rhesus	Multimale	Male: Mounts up, touches hindquarters, attempts to mount; Female: Presents hindquarters	LME	58-1.0/hr	Hours to more than a week	Seasonal	Pronounced perineal reddening with slight swelling	29	167	12	43.3	Hrdy and Whitten, 1987; Malnick and Pearl, 1987; Fooden, 1980; Shively et al., 1982; Chevalier-Skolnikoff, 1975; Smith, 1984; Andelman, 1986; Dixson, 1986; Harvey and Clutton-Brock, 1985
Toque	Multimale(?)	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters	MME(?)	-	Hours to days(?)	Seasonal	Prominent swelling of the perineum	30	-	-	-	Malnick and Pearl, 1987; Fooden, 1980; Smith, 1984; Andelman, 1986; Hrdy and Whitten, 1987

TABLE 6.1. Continued.

Species (Vernacular)	SOCIAL: Mating System	SOCIAL: Solicitation Behaviour	SOCIAL: Copulation Pattern	SOCIAL: Ejaculation Frequency	SOCIAL: Consortship Duration	SOCIAL: Breeding/Birth Seasonality	SEXUAL: Sex Skin (Oestrous)	SEXUAL: Cycle Length (Days)	SEXUAL: Gestation Length (Days)	SEXUAL: Interbirth Interval (Months)	SEXUAL: Age at First Living Birth (Months)	Source
M. fascicularis Group (Fooden, 1969)												
Toque	Multimale	Male: Touches hindquarters, attempts to mount(?); Female: None	SME	-	Hours to days(?)	Seasonal	Slight reddening of the perineum	29	-	8-24	60-72(?)	Hrdy and Whitten, 1987; Fooden, 1988; Shively et al., 1982; Smith, 1984; Andelman, 1988; Melnick and Pearl, 1987
Assamese	Multimale(?)	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters(?)	SME(?)	-	Hours to days(?)	Seasonal	Slight swelling of the perineum	-	-	-	-	Melnick and Pearl, 1987; Fooden, 1988; Smith, 1984; Andelman, 1988
Burmal	Multimale	Male: Rapid tongue flicking; Female: Presents hindquarters	SME	10.2 4/hr	Hours to 10 days	Seasonal	Slight swelling and reddening of the perineum	28	162	-	48(?)	Hrdy and Whitten, 1987; Melnick and Pearl, 1987; Fooden, 1988; Shively et al., 1982; Chevalier Skolnikoff, 1975; Smith, 1984; Andelman, 1988; Harvey and Clutton-Brock, 1985
Thibetan	Multimale(?)	Male: Touches hindquarters, attempts to mount(?); Female: Presents hindquarters	SME(?)	-	Hours to days(?)	-	-	-	-	-	-	Melnick and Pearl, 1987; Fooden, 1988
M. Arctoides Group (Fooden 1969)												
Stumptail	Multimale	Male: Touches hindquarters, attempts to mount; Female: Presents hindquarters	SME	10.5 6/hr	None	Non-Seasonal	None	31	175	19.1-21.3	53.60.1	Hrdy and Whitten, 1987; Fooden, 1988; Caldecott, 1986; Shively et al., 1982; Brereton, this study; Chevalier Skolnikoff, 1975; Andelman, 1988; Harvey and Clutton-Brock, 1985

*-Figures provided are averages unless stated otherwise
MME-Multiple mount ejaculator
SME-Single-mount ejaculator
(?)-Uncertain accuracy of information
@-Figure provided by Harvey and Clutton-Brock(1985) appears unrealistically high.

Rosenblum, 1973; Dixson, 1977). In the Barbary macaque (Taub, 1980), males are single-mount ejaculators (SME). SME males normally reach ejaculation after 15-20 intromissive thrusts in a single mount. For the three remaining species, the Moor, Booted and Tonkean macaques, their copulation patterns are unknown.

Concerning the frequency of ejaculations, an average of 1.4/hr was recorded for the pigtail macaque (Chevalier-Skolnikoff, 1975). Copulation frequencies for the other species of this group were not found.

Consortship durations in the *M. silenus-sylvanus* group range from 1-93 minutes in the Barbary macaque, and from hours to 10 days in the pigtail macaque (Hrdy and Whitten, 1987). Most of the other species probably fall somewhere in between.

With breeding and birth seasonality, the Barbary macaque is the only species that can be considered seasonal (Smith, 1984; Andelman, 1986). The liontail, pigtail and Crested species are all non-seasonal, while the status of the remaining three is unknown.

Sexual Attributes

Obvious external signs of oestrus are common and appear to predominate through sex skin (Dixson, 1983; Smith, 1984; Hrdy and Whitten, 1987). In particular, female Barbary, liontail and pigtail macaques show well-developed swellings and reddening of the perineum.

Length of menstrual cycle ranges from 31 days in Barbary macaques to 40 days in the liontail macaque (Hrdy and Whitten, 1987). In between, female pigtails have a cycle length of 32 days, and female Crested macaques have a length of 34 days. The lengths of the other species are unknown.

When considering gestation length, 170 days seems to be the average for pigtails, 163 days for Moors, 176 days for Crested, and 171.8 days for

liontails (Vancatova et al., 1986; Harvey and Clutton-Brock, 1985; Melnick and Pearl, 1987). Although no data were located for the other species, their lengths should be similar.

For interbirth intervals, Crested macaques average 18 months, pigtail macaques 13.5 months, and Barbary macaques 14.39 months (Burton and Sawchuk, 1982; Hadidian and Bernstein, 1979; Vancatova et al., 1986; Harvey and Clutton-Brock, 1985). Again, information on the other species in this group were not found.

The last attribute to be considered for this group concerns female age at first giving birth. According to Harvey and Clutton-Brock (1985), pigtail macaques average 47.3 months, Barbary macaques 46 months, and Crested macaques 66 months. First birthing ages for the others are unknown.

M. Fascicularis Group

Social Attributes

This subdivision includes the crabeating, Japanese, rhesus, and Taiwan macaques (see Table 3.1). Like the previous group, their mating systems are multimale, with the possible exception of the Taiwan macaques about which very little is known (Hrdy and Whitten, 1987; Melnick and Pearl, 1987). However, they too are probably multimale.

Female solicitations usually involve hindquarters presentation, whereas male solicitations can include behaviour more extreme, such as sexual attacks as sometimes observed in Japanese macaques (Hrdy and Whitten, 1987). More normal behaviour, however, is touching a female's hindquarters and attempting to mount.

The males of this group are also MME, at least in Japanese and rhesus macaques (Fooden, 1980; Shively et al., 1982). Again, very little is known

about the Taiwan macaque, but the crabeating macaque appears to use a combination of both strategies in about equal proportions (Shively et al., 1982; Caldecott, 1986).

With ejaculation frequency, rhesus average 1.0-2.0/hr, crabeating macaques average .00-1.33/hr, while Japanese macaques average .50/day (Chevalier-Skolnikoff, 1975; Shively, 1982; Hrdy and Whitten, 1987). Frequency of copulations for Taiwan macaques is not known.

In crabeating, rhesus and Japanese macaques, consortships last from hours to more than a week. Because of the lack of knowledge of Taiwan macaques, consortship length in this species is unknown (Hrdy and Whitten, 1987).

Breeding and birth seasonality are interesting in this group because for the rhesus, Japanese and Taiwan macaques both are quite prominent and distinct (Smith, 1984; Andelman, 1986). In crabeating macaques, however, seasonality, as with copulation pattern, is not quite as clear cut. They have been observed to show both seasonal and nonseasonal patterns in different behavioural studies (Smith, 1984).

Sexual Attributes

Concerning sexual skin, females of all four species of this group show some external signs of oestrus (Hrdy and Whitten, 1987; Smith, 1984; Dixson, 1983). In Japanese macaques, reddening and swelling of the perineum increases with age, whereas just the opposite occurs in crabeating macaques. Taiwan females show only prominent swellings, while rhesus females show a moderate amount of reddening and some swelling.

Cycle lengths range from an average of 28 days in the Japanese to an average of 31 days in the crabeating macaque (Hrdy and Whitten, 1987). Taiwan macaques cycle on an average of every 30 days and rhesus every 29

days (Hrdy and Whitten, 1987; Harvey and Clutton-Brock, 1985).

Gestation lengths are also quite similar among the species of this group. Crabeating macaques average 162 days, rhesus average 167 days, while Japanese average 173 days (Harvey and Clutton-Brock, 1985). No information is available on gestation length for Taiwan macaques.

For intervals between births, crabeating macaques average 13 months, whereas rhesus average 12 months (Harvey and Clutton-Brock, 1985). Interbirth intervals for Japanese and Taiwan macaques are probably similar.

Averages for age at first giving birth are 46.3 months in crabeating macaques, 60 months in Japanese macaques, and, in rhesus, 43.3 months (Harvey and Clutton-Brock, 1985). Once again, information on Taiwan macaques is unavailable.

M. Sinica Group

Social Attributes

Like the last, this subdivision also includes four individual species. They are the Toque, Assamese, Bonnet, and Thibetan macaques (Table 3.1). From the information available, the multimale mating system is standard (Hrdy and Whitten, 1987; Melnick and Pearl, 1987). The system definitely exists for the Toque and Bonnet macaques, and is probably the same system employed by the Assamese and Thibetan species.

Solicitation behaviour in the group is practised by both males and females (Hrdy and Whitten, 1987). Females present their hindquarters in Bonnet macaques, while, also in Bonnets, males sometimes initiate mounts by tongue flicking rapidly. Males are usually the initiators in Toque macaques.

When considering copulation pattern, rather than being MME, the males

of this group are classified as SME (Fooden, 1980; Shively et al., 1982). In one study of Bonnets, for example, over 90% of the copulations consisted of single mounts (Shively et al., 1982). Toque macaques are also SME, while the copulatory patterns for Assamese and Thibetan macaques are unknown.

For ejaculation frequency, Shively et al. (1982) found that Bonnets range from .18 to 2.4 ejaculations per hour of observation. Chevalier-Skolnikoff (1975) quoted a rate of 1.0-2.0/hr. Rates for the other species are not available.

Also, for Bonnet macaques, consortship durations last from several hours to 10 days (Hrdy and Whitten, 1987). Durations for the three other species are unknown.

The Toque, Assamese and Bonnets are all seasonal in breeding and in giving birth (Smith, 1984; Andelman, 1986). It is unknown whether the Thibetan macaque is seasonal or non-seasonal.

Sexual Attributes

With development of sex skin during oestrus, this group, as a whole, unlike the previous two, shows diminished swelling and reddening (Dixson, 1983; Hrdy and Whitten, 1987; Smith, 1984; Melnick and Pearl, 1987). Perineal swelling in both Bonnets and Assamese is slight, and reddening is minimal in Bonnet and Toque macaques.

Cycle lengths for females of the *M. Sinica* group are similar to the others. Toque females average 29 days between cycles, while Bonnets average 28 days, with a range of 25 to 36 days (Hrdy and Whitten, 1987; Harvey and Clutton-Brock, 1985). The others are unknown.

The average length of gestation for female Bonnets is 162 days, and the range is 153 to 169 days (Harvey and Clutton-Brock, 1985; Melnick and

Pearl, 1987). Similar information on Toque, Assamese and Thibetan macaques is unavailable.

A figure for interval between births could be found only for the Toque macaque. According to Melnick and Pearl (1987), Toque females range from 8 to 24 months between births.

Finally, the only figures located for age at first giving birth are figures of maturation, which may not be the same. Females mature anywhere from 5 to 6 years (60-72 months) in Toque macaques, and average 4 years (48 months) in Bonnet macaques (Melnick and Pearl, 1987).

M. Arctoides Group

Social Attributes

The final *Macaca* subdivision to be reviewed includes a single species: the stumptail macaque (Table 3.1). Like others, its mating system is multimale (Hrdy and Whitten, 1987). Both males and females are also involved in solicitations. Females solicit by presenting, while males solicit by touching the hindquarters of a female and attempting to mount (Hrdy and Whitten, 1987; personal observation).

Like the other groups, the stumptail copulatory pattern is SME (Fooden, 1980; Hrdy and Whitten, 1987; Caldecott, 1986; Shively et al., 1982). Furthermore, ejaculation frequency averages .18-5.0/hr (Brereton, this study; Chevalier-Skolnikoff, 1975), and consortships (Hrdy and Whitten, 1987; personal observation) and breeding and birth seasons have not been seen (Smith, 1984; Andelman, 1986).

Sexual Attributes

With sex skin, even though very slight perineal swellings and reddening occurs at midcycle in some individuals, overall, it is undetectable by human observation (Hrdy and Whitten, 1987; Dixson, 1983; Smith, 1984). Average cycle length is 31 days (Hrdy and Whitten, 1987), length of gestation averages 175 days (Harvey and Clutton-Brock, 1985), and 19.1 and 21.3 months are the mean intervals between births (Estrada and Estrada, 1981; Brereton, this study). Finally, female age at first giving birth averages 53 and 60.1 months (Estrada and Estrada, 1981; Brereton, this study).

DESCRIPTION OF STUMPTAIL MATING, COPULATORY TIE, AND GENITALIA MORPHOLOGY

With the background of the previous section, the socio-sexual behaviour of stumptail macaques will now be looked at more closely, as will their specialized genitalia. This background may help explain why sexual interference occurs at such a high rate in stumptails when compared with other species, as outlined in Chapter 7.

Mating Description

As noted earlier, stumptails of both sexes solicit mating (Hrdy and Whitten, 1987; personal observation). This period is known as the approach phase (Chevalier-Skolnikoff, 1975). A female solicits by approaching a male and then turning and presenting her hindquarters. She also maintains eye contact with the male throughout. When a male solicits, besides approaching a female while staring at her, he often displays a facial expression known as the teeth-chatter grimace (see Appendix). At this

stage, the female may attempt to escape, but when he is within arms length, she will usually let him make contact with her anogenital region.

After he examines her hormonal state either visually, manually, orally, or olfactorally, or any combination thereof, and remains interested, while she continues to cooperate, the male mounts her using a double foot clasp of her hindlegs while grasping her back and hips with his hands (see Figures 7.2 and 7.3). As she supports his weight, intromission is made and thrusting begins. This continues for up to 170 thrusts before ejaculation is reached. Rarely is ejaculation accomplished in less than 15 thrusts or more than a single mount.

The copulation can be divided into three phases: pre-ejaculatory, ejaculatory, and post-ejaculatory (Chevalier-Skolnikoff, 1975). The pre-ejaculatory phase includes the interval between first intromission and the male reaching ejaculation. It spans a period of from 20 to 180 seconds and is often accompanied by grunting vocalisations and teeth-chatter grimacing by the male, and occasionally by the female. The female will also sometimes reach back with one hand to grasp at the male while staring at him.

The ejaculatory phase, as its name implies, culminates in ejaculation by the male. Its distinguishing features are a sudden pause in male thrusting, followed by his body becoming stiff. This is usually accompanied by a frown-round-mouth (Appendix) and a low to medium pitched rhythmical expiration vocalization. At this point, the female may also display a frown-round-mouth and vocalise rhythmically. Furthermore, she may reach toward the male, but, more likely, she will remain facing forward while teeth-chatter grimacing.

In the post-ejaculatory phase, also known as the tie or sit-back phase, the male steps down from the female's hindlegs and either remains standing,

while grasping her sides or back with his hands, or more commonly, sits back on the ground as he grasps the female in his lap. However, regardless of the position, intromissive genital contact continues and is kept for up to 120 seconds. As it is kept, the pair may groom each other or just sit. But either way, they both appear to be involved in a "genital tie" (Lemmon and Oakes, 1967), unable or unwilling to separate (see below). When separation finally does occur, they often move apart a meter or more while the female inspects her hindquarters and the male eats his coagulated ejaculate.

Copulatory Tie

The apparent genital tie observed in stumptail macaques is unique among Old World monkeys (Dixson, 1987a), rare among primates (Dixson, 1987b), and may be similar to the genital lock found in canids (e.g., Kleiman and Eisenberg, 1973; Woolpy, 1968). First reported by Lemmon and Oakes (1967), the tie appears to occur when the glans penis (see Figure 6.1B) increases markedly during ejaculation after it has passed under the sphincter-like vestibular colliculis (Figures 6.2A and B) of the female's perineum (Fooden, 1967). Even though the tie in stumptails has been questioned by some researchers (Goldfoot et al., 1975; Linnankoski et al., 1981; Bernstein, 1980; Blurton Jones and Trollope, 1968), its likelihood is increased by the fact that many cone-shaped projections (Figure 6.1A) exist on the surface of both the glans and corpus penis (Kanagawa and Hafez, 1973). This may act as adhesion against withdrawal at the time of ejaculation and for a short time (up to 120 seconds) thereafter. Crabeating macaques also have these cone-like projections (Kanagawa and Hafez, 1973), as do rhesus macaques (Herbert, 1974) and talapoin monkeys *(Cercopithecus talapoin)* (Dixson and Herbert, 1974). However, in these

species, the projections are much smaller in size (e.g., .05-0.1 mm in crabeating macaques, compared with 3-4 mm in stumptails), and tying has not been seen.

In the greater galago *(Galago crassicaudatus)* (Dixson, 1976), where penile "spins" are relatively large, and even rough to the touch, tying does exist. These spines may also serve the purpose of adhesion. According to Dixson (1976) and Charles-Dominique (1977), backward directed spines function as an anchor for prolonged intromission. Penile projections may have a similar function in stumptails, which may, in turn, serve to increase the likelihood of conception (Dixson, 1987b). Speculation on just how this may occur will be addressed below.

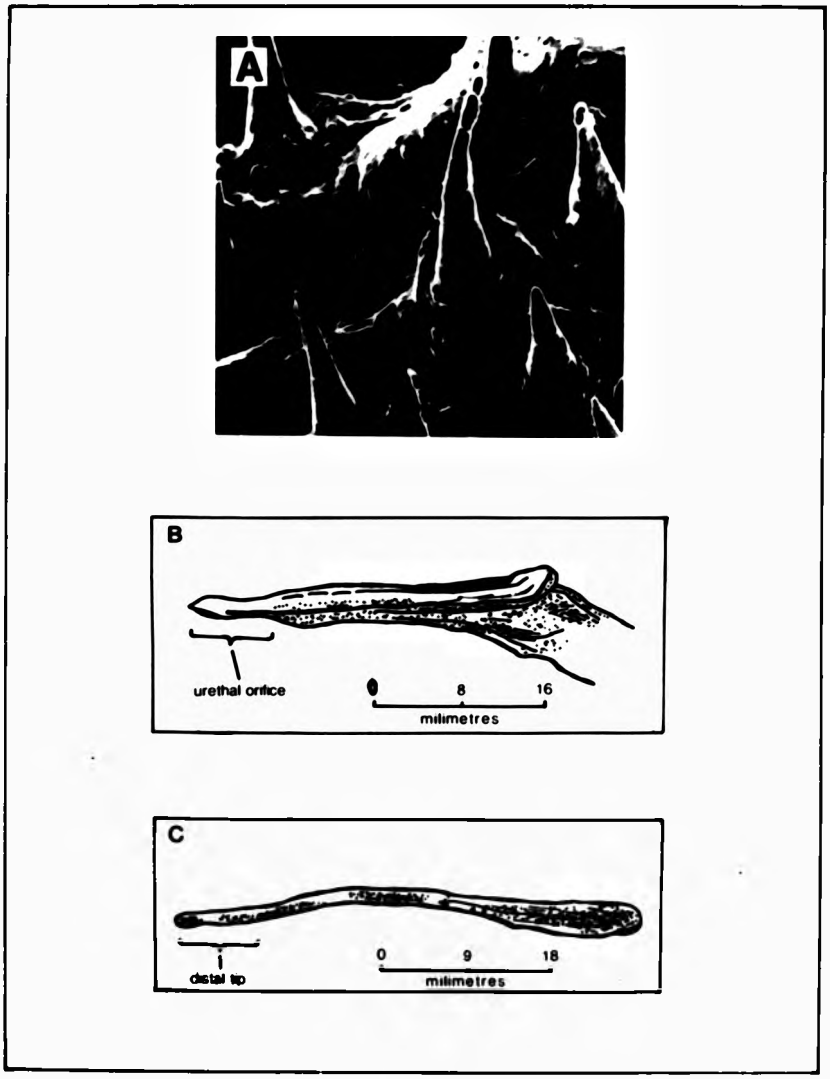
Genitalia Morphology

Besides penile projections, the anatomical features of stumptail genitalia differ from other species of macaques in specific ways. The exact reasons for these differences remain speculative. One hypothesis, proposed by Fooden (1967), suggests that the structural specialisation of stumptail genitalia developed to prevent hybridisation with sympatric species, most likely the rhesus macaque. However, with copulatory patterns as they are in stumptails, namely male capacity for frequent ejaculation and prolonged post-ejaculatory intromission, sexual selection is probably a more likely explanation (Dixson, 1987b). More will be said about this in Chapter 10.

Male

The glans penis of male stumptails (Figure 6.1B) differs substantially from that of other macaques (Fooden, 1967, 1976; Michael et al., 1973; Kanagawa et al., 1972). It is dorso-ventrally flattened and lanceolate-like, being long (50-70 mm) and slender (10 mm at the base to 5 mm at the tip),

FIGURE 6.1. Genitalia morphology of male Macaca arctoides. (A) Cone-like projections on the glans and corpus penis (x100)(from Kanagawa and Hafez, 1973). (B) Glans penis (adapted from Fooden, 1967). (C) Baculum (adapted from Fooden, 1967).



rather than short (25 mm) and helmet-like as in other macaques.

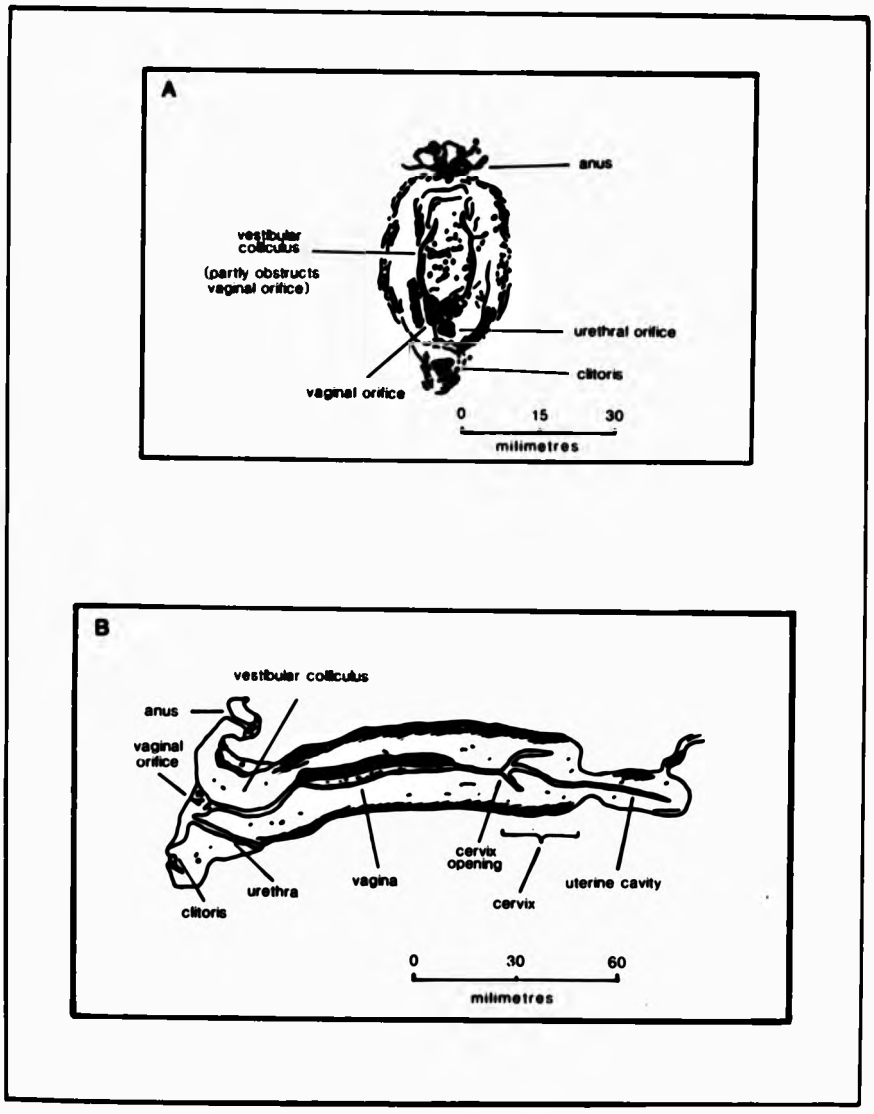
Baculum (or penis) length is also different from other species of macaques, or from primates in general, in that it is long for their body weight (see Figure 6.1C). According to Dixson (1987b), the average length of stumptail baculum is 52.82 mm. This compares with 11-26.2 mm for Barbary, Moor, crabeating, and Assamese macaques, 6.9 mm for chimpanzees, and 14.8 mm for orangutans. Greater galagos have an average baculum length of 22.4 mm, which is also quite long considering their lesser body size. However, they too, like stumptails, maintain intromission for prolonged periods during the post-ejaculatory phase of copulation. So baculum length and the prolonged copulatory pattern appear to be related, and, together, may contribute to the greater likelihood of conception in both species (Dixson, 1987b).

As to how this could occur, it may be that baculum length in stumptails facilitates semen delivery directly into the female's cervical canal. Also, prolonged intromission may provide the distal tip of the baculum (Figure 6.1C) with an opportunity to position the cresent-shaped copulatory plug produced in this species in a conceptually conducive position at the entry of the cervix (Figure 6.2B) (Dixson, 1987b). The accuracy of these speculations and the exact mechanisms responsible await further research.

Female

A major difference between female stumptail genitalia and that of other macaques is that in stumptails "the vaginal orifice is partly obstructed by a mid-dorsal ellipsoid structure, the vestibular colliculus, which protrudes from the roof of the vaginal introitus" (Michael et al., 1973). Furthermore, the cervical colliculi, common in other species, is not found in stumptail females. Finally, the urethral orifice in stumptails is in a more external

FIGURE 6.2. Genitalia morphology of female Macaca arctoides. (A) Perineum (adapted from Fooden, 1967). (B) Cross-section of genital canal (adapted from Fooden, 1967).



position nearer the clitoris than in other macaques (see Figure 6.2B). This is apparently to accommodate for an overhanging vestibular colliculus (Fooden, 1967).

When looked at together, then, both male and female genitalia in stumptails are clearly complementary. The slender and tapered glans penis of the male "...is ideally formed for reaching and entering the vaginal opening of the female by passing through the narrow slit under the vestibular colliculus" (Fooden, 1967:940). The possible reasons for this coevolution were briefly mentioned above. But, regardless of the reasons, the genital morphology of male and female stumptails represent an evolutionary unique form when compared with other species of macaques (Fooden, 1967).

RESULTS

Although stumptails vary somewhat in their overall pattern of mating from other species of macaques, as noted earlier, they appear relatively consistent within their own species. The general results of mating behaviour from this study will now follow.

Group

The total matings recorded during this study were 113. The days they were observed and the number recorded for each of these days are listed in Table 4.3. Figure 6.3 shows mating distribution over the months of observation, and Figure 6.4 shows their distribution throughout the hours of the day.

As can be seen from Figure 6.3, most of the matings occurred in the month of February, 1984 (51%, N=58). The two months of January and

FIGURE 6.3. Matings by month.

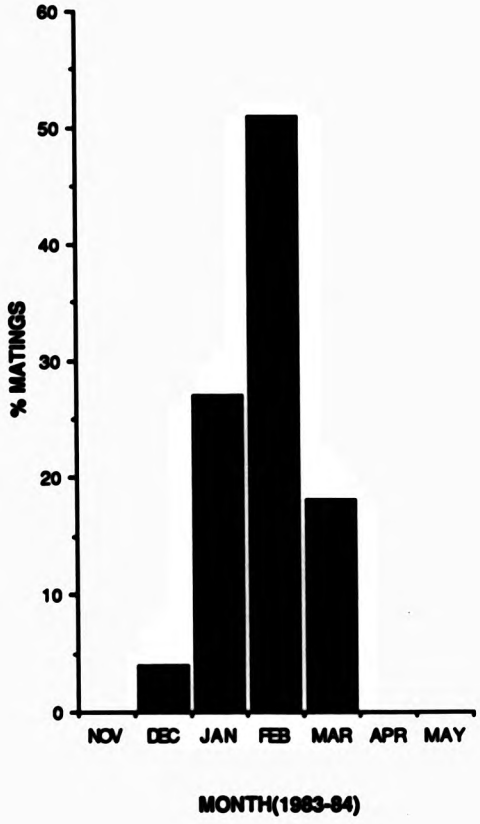
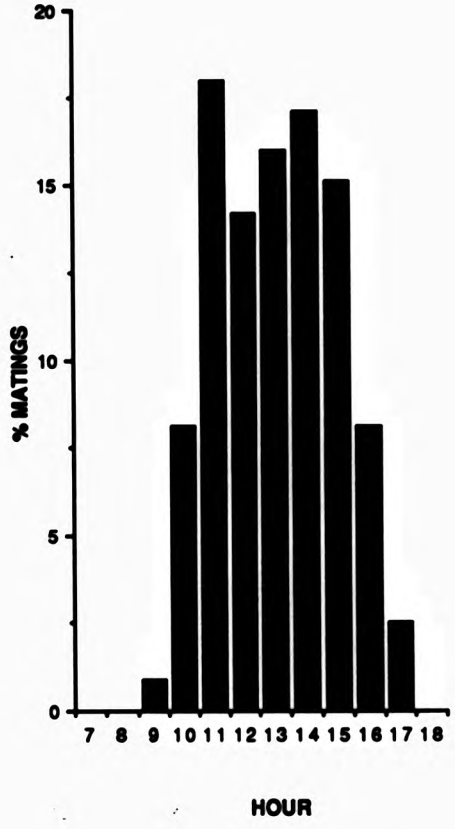


FIGURE 6.4. Matings by hour of the day.



March had 45% (N=51), while 4% (N=4) were recorded in December, 1983. No matings were seen in the months of April and May, 1984. As listed in Table 4.3, the percentage of observation hours spent on the island varied from 6% in December to 30% in February, with only 11% in April and 7% in May. This may have partly contributed to the discrepancy between months.

Concerning mating distribution by hour, when the day is split into two halves, 27% (N=30) of the matings occurred in the morning and 73% (N=82) occurred in the afternoon. An exact time for 1 of the 113 matings was not recorded. When grouped according to days on which these matings occurred (27 of 83, or 33%) (Table 6.2), a Sign test shows the morning and afternoon difference not to be significant at the .05 confidence level (p=.077, 2-tailed). It should be noted, however, that of the 600 observation hours spent on the island, 334 (56%) were in the morning, while only 266 (44%) were in the afternoon. So a trend does exist toward afternoon matings.

The frequency of mating can be calculated in one of several ways. For example, when the number of matings (N=113) per observation day (N=83) are considered, the mean is 1.36/day. Another way of calculating, however, is number of matings (N=113) per observation hour (N=600). When this is done, the mean is .19/hr. The latter calculation is the more useful. Furthermore, if calculated by number per hour in a series (multiple matings), the mean is 3.16/hr, with 4.59 matings occurring per series (range: 1-14).

Similarly, on the 27 days that matings were recorded in this study, multiple matings were observed on 18 (66%) of these days. The number of matings involved were 104 (92%) leaving only 9 (33%) days where single matings occurred. On 9 (50%) of the multiple matings days, 2 or more

TABLE 6.2. Percent of matings observed in the morning and afternoon by day.

DAY/MONTH (1983-84)	% MATINGS MORNING (N)	AFTERNOON (N)
22/12	100(3)	0
27/12	0	100(1)
04/01	100(2)	0
05/01	0	100(1)
13/01	60(3)	40(2)
17/01	100(2)	0
19/01	0	100(1)
20/01	100(3)	0
24/01	50(1)	50(1)
25/01	0	100(14)
31/01	0	100(1)
02/02	100(1)	0
04/02	0	100(4)
06/02	0	100(11)
10/02	0	100(4)
13/02	0	100(2)
15/02	71(5)	29(2)
16/02	11(1)	89(8)
17/02	0	100(4)
20/02	0	100(1)
21/02	0	100(2)
29/02	31(4)	69(9)
01/03	100(1)	0
14/03	0	100(1)
20/03	0	100(4)
21/03	0	100(1)
31/03	33(4)	67(8)

(N)=number of matings

males or females were involved in mating.

Information collected before and after mating is of further interest. Of the 113 matings, 18 (16%) were preceded by the female initially trying to avoid the male. This involved as little as moving away to outright fleeing when approached [see Avoid and Flee (Pre-Mount), Appendix]. After mating, 81 (72%) consisted of the female (32, or 28%), the male (20, or 18%), or both (29, or 26%) immediately moving 5 metres or more from the physical location where the mating took place. Six matings (5.2%), out of the 113, also ended early (see Break Tie, Appendix). Furthermore, the mean interval between matings in a series was 19 minutes (range: 5-156).

Figure 6.5 graphs several mean durations in seconds, one-zero behaviour frequencies (Appendix), and number of mounts to ejaculation for the 113 matings. As noted, the average duration for each mating was 97.32 seconds. This, in turn, was broken down into before and after ejaculation. The mean duration up to ejaculation was 27.85 seconds, and the average tie was 69.47 seconds long. The average number of one-zero occurrences of typical male and female mating behaviour was 17.58. The mean number of mounts to reach ejaculation was 1.48, and the typical mating female would look back, reach back, or a combination of the two (see Appendix) 46% (N=52) of the time.

Individual

Mating distribution among individuals showed marked variation. Of the 8 males seen to mate, the 2 highest ranking, Pancho and McGregor (Table 6.3), participated in 104 of the 113 (92%) matings recorded (Figure 6.6). Of these, Pancho (the alpha male) mated 78 (75%) times, while McGregor (the beta male) mated 26 (25%) times. The other 6 lesser ranking males were observed mating only 9 (7.94%) times. A Chi Square test shows

FIGURE 6.5. Mating behaviour averages. MAT DUR = Duration of Mating, TO EJAC = Duration to Ejaculation, TIE = Tie Duration, MAT BEH M+F = Frequencies of Male's Plus Female's One-Zero Behaviour, MOUNTS = Number of Mounts to Ejaculation. Durations are in seconds. T-bars represent top half of Standard Error.

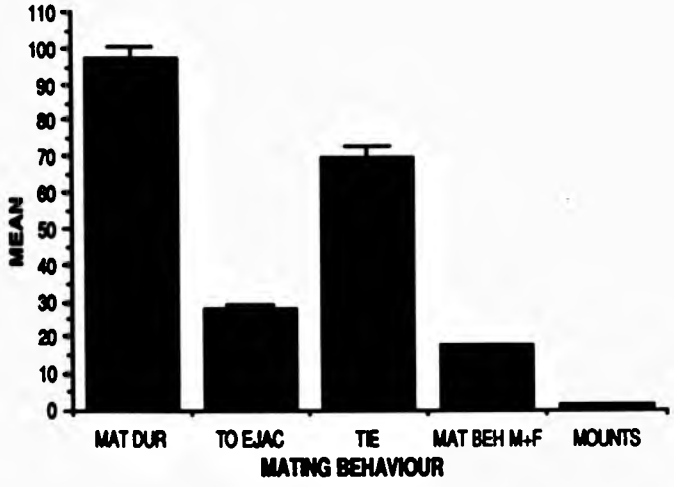
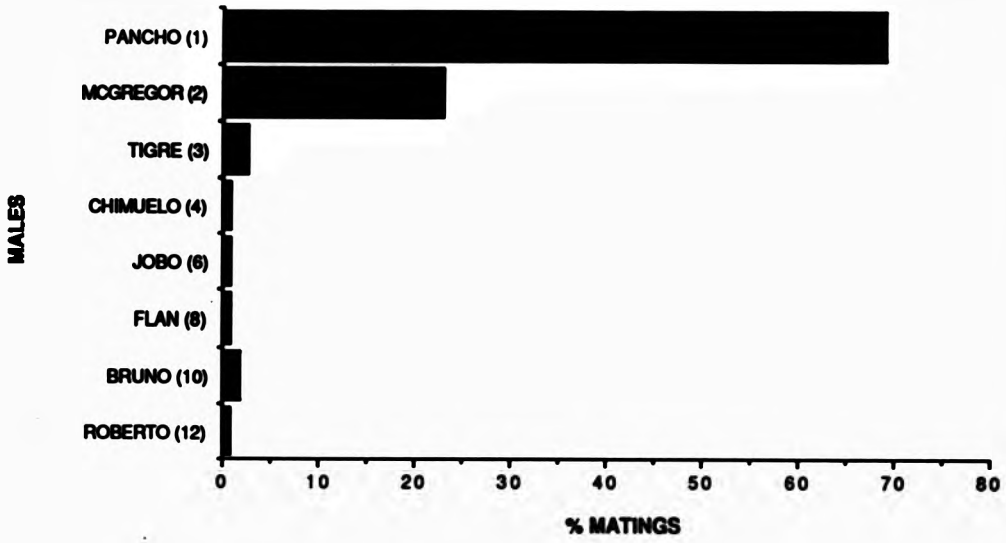


TABLE 6.3. Male dominance rank order matrix. Determined by dyadic agonistic encounters.

ACTOR \ RECIPIENT	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Pancho (1)	*	15	23	5	3	1	14	4	7	2	5	3	4	3			2					
Mcgregor (2)		*	11	15	1	3	11	6	1	3	2	1	1	4	2				1	2		
Tigre (3)			*	11	7	8	7	5	3	6	9	4										
Chimuelo (4)				*	1	5	4	6	3	3	10	4		2	2	1		1	1			
Luciano (5)					*	8			3	1	15	1				1			1			
Jobo (6)						*	3		1		11	4		1								
Santos (7)					1		*	12	7	8	1	3		1	1	1						
Flan (8)					1			*	9	9	3	2		6		1		1				
Blair (9)									*	8	4	6	6	6	5				4			
Bruno (10)						1				*	2	4	2	2	2	3	1	1	1			
J.D. (11)											*			2	3	4			1			
Roberto (12)												*		1	3	1						
Bruto (13)													*		2	3		2	1			
Wilfrido (14)														*	3	1		1	1			
Mario (15)															*				1			
Lorenzo (16)																*			2			
Miguelito (17)																	*		1			
Florencio (18)																		*	1			
Blas (19)																			*			
Teo (20)																				*		
Martin (21)																					*	
Millo (22)																						*

N=467

FIGURE 6.6. Male mating distribution. Listed by dominance rank order.



these differences to be highly significant (x^2=366.78, p<.001). Although different, mating distribution among females was also highly significant (x^2=69.39, p<.001) (Table 6.4 and Figure 6.7). Pierre, with an overall female rank of 5, and Lucia, Bruja and Rosy, ranked 14, 15 and 21 respectively, together participated in 85 (75.22%) of the 113 matings. The other 6 variously ranked females participated in the remaining 28 (24.78%) matings. It is obvious than that a strong correlation exists between male rank order and the number of matings each participated in (Spearman rank correlation coefficient test, r_s=.783, p=.016). With females, however, rank order and number of matings are not correlated (r_s=.185, p>.05). But, as noted above, mating among females is not equally distributed (Figure 6.7 and Table 6.5). The fact that some of the females were pregnant during the course of the study (e.g., Ucilia, Canela), as revealed from later birth records, may help explain this result. Some females may have also been too old to conceive (e.g., Jarocha, Blondie). If these females had mated, it is unknown how they would have effected the association between female rank and mating frequency.

With association, affiliation duration and mating frequency are also highly correlated (r_s=.714, p<.05) (Table 6.5 and Figure 6.8). In other words, the greater the affiliation time an adult male and female have with each other, the more frequently they mate. No correlations exist, however, between either mating frequency and male or female age (r_s=-.274, p>.05 and r_s=.277, p>.05 respectively), or between mating frequency and parity (r_s=.476, p>.05). Also, matings between males and females from the same matriline were not observed.

TABLE 6.4. Female dominance rank order matrix. Determined by dyadic agonistic encounters.

ACTOR \ RECIPIENT	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Jarocha (1)	•	1	3		13	6	3	6		1	3	3	3	4	5	4		2	2	5	2		2			1				1						
Marcela (2)		•	2	1						3							2	1				1	2							1						
Martha (3)		1	•	4	2	1	3			4	3			3	1						1		4	2												
Mirna (4)				•	2	2	4	2	1		4	1	2	3	2	2	2	1	1		1	1	3			1										
Pierre (5)		1	1		•	3	2			4	4			5	2			1	2			2	6	3												
Flaca (6)						•	3	1	1		1	5	4	3	1				1	3			2		1											
Fanny (7)						1	•	8	3		1	2	8	2	1		1		2	1		3	2													
Elena (8)			1					•			1	2	2	4	5				1	4	2		2			1									
Negra (9)		1							•	1			3				1	1	3	2	2	2	3													
Enriqueta (10)										•	2	11	4	2		5	3	1		3		1	2	1				1	1						
Blondie (11)								1			•	1	2	7	3	2	1		3	4	5	4	8	1			1			1	1					
Flavia (12)												•	2				3	1				1	1			1									
Ucilia (13)											1		•		1		1	3	1	1			1	1											
Lucia (14)												1		•	3				5	3	1	5	4			1	1								
Bruja (15)								2							•		1	1	4	6	3	3	5			1		1							
Piedad (16)																•	1						1												
Blasita (17)																	•	1				1		1			2			2					
Flossie (18)																		•	3	1		1				4									
Canila (19)																			•	4	3	1	1		1										
Lolita (20)																				•	5	2	4	1		5									
Rosy (21)																					•	1	3	7		1									
Blanca (22)																						•	4	1											
Teresa (23)																	1					1	•			1									
Juanita (24)																								•											
Miriam (25)																									•										
Sigri (26)																										•				1					
Elpidia (27)																											•								
Rosa (28)																												•							
Florinda (29)																													•	1					
Brisa (30)																														•					
Lupita (31)																															•				
Lourdes (32)																																•			
Blonny (33)																																	•		
Blenda (34)																																		•	
Elsa (35)																																			•
Julieta (36)																																			

N=507

FIGURE 6.7. Female mating distribution. Listed by dominance rank order.

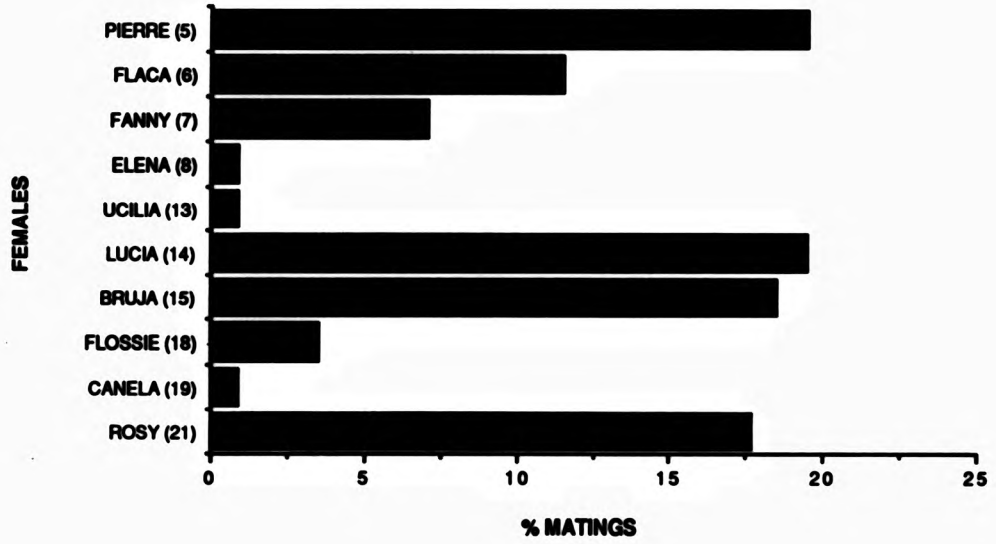
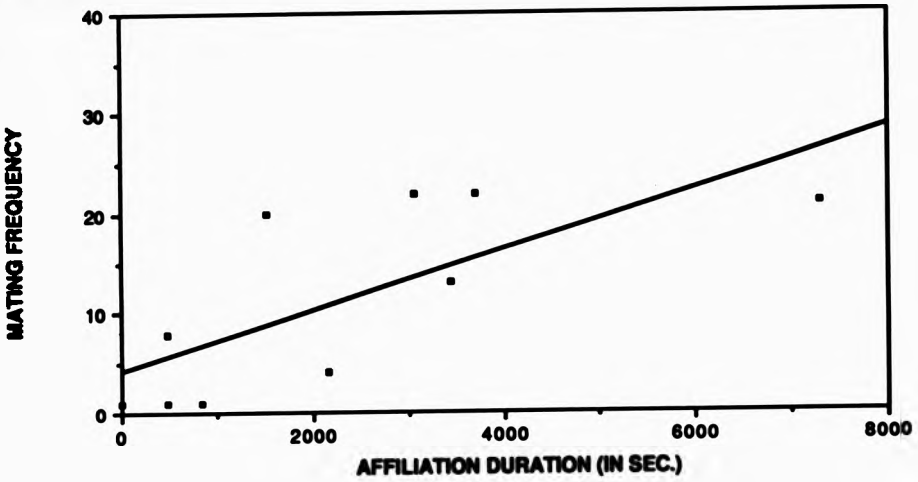


TABLE 6.5. Mating female/male affiliation durations (in seconds) and their mating frequencies. Percentages for both are in parenthesis. Subjects are listed by rank order.

	MALES							
FEMALES	Pancho(1)	Mcgregor(2)	Tigre(3)	Chimuelo(4)	Jobo(6)	Flan(8)	Bruno(10)	Roberto(12)
Pierre(5)	3003(98%)	-	67(2%)	-	-	-	-	-
	21(95%)	-	1(5%)	-	-	-	-	-
Flaca(6)	347(10%)	3111(90%)	-	-	-	-	-	-
	6(46%)	7(54%)	-	-	-	-	-	-
Fanny(7)	476(100%)	-	-	-	-	-	-	-
	8(100%)	-	-	-	-	-	-	-
Elena(8)	-	-	-	487(100%)	-	-	-	-
	-	-	-	1(100%)	-	-	-	-
Ucilia(13)	-	-	-	-	-	-	-	?(?%)
	-	-	-	-	-	-	-	1(100%)
Lucia(14)	1774(48%)	1319(36%)	611(16%)	-	-	-	-	-
	19(86%)	2(9%)	1(5%)	-	-	-	-	-
Bruja(15)	291(4%)	6552(90%)	-	-	499(6%)	-	-	-
	8(38%)	12(57%)	-	-	1(5%)	-	-	-
Flossie(18)	-	-	751(35%)	-	-	392(18%)	1020(47%)	-
	-	-	1(25%)	-	-	1(25%)	2(50%)	-
Canela(19)	-	849(100%)	-	-	-	-	-	-
	-	1(100%)	-	-	-	-	-	-
Rosy(21)	233(15%)	1288(85%)	-	-	-	-	-	-
	16(80%)	4(20%)	-	-	-	-	-	-

FIGURE 6.8. Correlation scattergram of affiliation duration with mating frequency.



COMPARISONS AND DISCUSSION

These results will now be compared with results from other studies. Table 6.6 provides a summary. Where differences occur, they may be attributed to the marked variation in research settings, with this project and the Estrada's representing the most naturalistic. The other studies were carried out on captive subjects. However, the results overall are quite similar.

Group

As noted earlier in the chapter, a mating season for stumptails has not been seen, and matings occur commonly throughout the year (Estrada and Estrada, 1976a, 1981; Fooden et al., 1985; Nieuwenhuijsen et al., 1985; Smith, 1984; Trollope and Blurton Jones, 1975; Hill, 1974). In this study, even though matings were not seen during the months of April and May, possibly because of reduced hours of observation, it is assumed based on other's observations that mating seasonality also does not exist on Tanaxpillo (Estrada and Estrada, 1981; Caba-Vinagre, personal communication).

For frequency of mating, Bernstein (1980) found that stumptails mate at a rate of 0.3/hr, where in this study the hourly rate was 0.19. If mating occurred in a series, however, the rate in the present study was 3.16/hr, compared with 5.0/hr reported by Chevalier-Skolnikoff (1975). Also, when matings occurred in a series, as they often did (104 out of 113, or 92%), the average number per series was 4.58. The average per series in the study by Estep et al. (1984) was 5.6. Chevalier-Skolnikoff did not give an average number per series, but did report that 53 (78%) of 68 matings occurred in a series of 3 or more. Furthermore, multiple matings occurred

Behaviour	SOURCES						
	Brereton (this study)	Estrada and Estrada('76a,'81), Fooden('85), Nieuwenhuijsen et al('85), Smith('84), Trollope and Blurton Jones('75), Hill('74)	Estep et al('84), Estep et al('88)	Bernstein('80)	Chevalier-Skolnikoff('75)	Niemeyer('80), Niemeyer and Chamove ('83), Bruce('84)	Gouzoules('74)
GROUP							
Matings	113	33(a) 24(b) 682(c) 346(d)	146 616	-	68	271 618(e)	97
Monthly Distribution	Dec-4 Jan-31 Feb-58 Mar-20(f)	Throughout year	-	-	-	-	-
Hourly Distribution	9-1 10-9 11-20 12-16 13-18 14-19 15-17 16-9 17-3(g)	-	-	-	-	-	-
Days Matings Observed	27 of 83	-	26 of 59	-	-	-	-
Mating Frequency	1.36/day .19/hr 3.16/hr(series)	-	-	.3/hr	5.0/hr(series)	-	-
Matings Per Series	4.62	-	5.6	-	3+	-	-
Multiple Mating Days	18 of 27	-	20 of 26	-	-	-	-
Matings Involved in Series	104 of 113	-	-	-	-	-	-
Multiple Mating Days Involving 2 or More Males/Females	9 of 18	-	-	-	-	-	-
Pre-Matings Females Attempt to Avoid Males	18 of 113	-	-	-	-	-	-

TABLE 6.6. Continued.

Behaviour	Brereton (this study)	Estrada and Estrada('76a,'81), Fooden('85), Nieuwenhuijsen et al('85), Smith('84), Trollope and Blurton Jones('75), Hill('74)	Estep et al('84), Estep et al('88)	Bernstein('69)	Chevalier-Skolnikoff('75)	Niemeyer('80), Niemeyer and Chamove ('83), Bruce('84)	Gouzoules('74)
	SOURCES						
Post-Matings Male/Female/Both Move 5 Metres+ From Mating Location	81 of 113	-	-	-	-	-	-
Matings Terminated Early	6 of 113	-	-	-	-	-	-
Pre-Ejaculation Duration(h)	27.85	-	16.8	-	59.0	35.5	-
Post-Ejaculation Duration(h)	69.47	-	88.8	-	114.0	70.8 85.8(e)	-
Mating Duration(h)	97.32	-	105.6	-	168.0	106.3	-
One-Zero Male/Female Mating Behaviour	17.58	-	-	-	-	-	-
Matings Female Looks/Reaches Back(or Both)	52 of 113	-	-	-	-	-	-
Mounts to Ejaculation	1.43	-	-	-	-	-	-
Inter-Mating Interval (Series)	19.0	-	14.33	-	-	-	-
INDIVIDUAL							
Male Mating Distribution(j)	Panchio-78 McGregor-26 Tigre-3 Chimuelo-1 Jobo-1 Flan-1 Bruno-2 Roberto-1	-	Monopolised by Alpha Male	-	-	Monopolised by Alpha Male(k)	Monopolised by Alpha Male

TABLE 6.6. Continued.

Behaviour	Brereton (this study)	Estrada and Estrada('76a,'81), Feeden('85), Nieuwenhuijsen et al('85), Smith('84), Trollope and Blurton Jones('75), Hill('74)	Estep et al('84), Estep et al('86)	Bernstein('86)	Chevalier-Skolnikoff('75)	Niemeyer('80), Niemeyer and Chamove ('83), Bruce('84)	Gouzoules('74)
		SOURCES					
Female Mating Distribution(j)	Pierre-22 Flaca-13 Fanny-8 Elena-1 Ucilia-1 Lucia-22 Bruja-21 Flossie-4 Canela-1 Rosy-20	-	Non-Random	-	-	-	-
Male Affiliation Durations with Females(h)(j)	Pancho-6124 McGregor-13119 Tigre-1429 Chimuelo-487 Jobo-449 Flan-392 Bruno-1020 Roberto-?	-	-	-	-	-	-
Female Affiliation Durations with Males(h)(j)	Pierre-3070 Flaca-3458 Fanny-476 Elena-487 Ucilia-? Lucia-3704 Bruja-3704 Flossie-2163 Canela-849 Rosy-849	-	-	-	-	-	-
Male/Female Mating/Age Association	Unrelated	-	Unrelated	-	-	-	-
Mating/Parity Association	Unrelated	-	Unrelated	-	-	-	-
Matings Between Males/Females from Same Matriline	None	-	-	-	-	-	-

*-Numbers either equal raw data or means, the difference is self-evident
(a)-Fertile matings (Estrada and Estrada, 1976a)
(b)-Fertile matings (Estrada and Estrada, 1981)
(c)-Mounts with and without ejaculation are not distinguished (Smith, 1984)
(d)-Trollope and Blurton Jones (1975)
(e)-Bruce (1984)
(f)-Non-seasonality is a reasonable assumption based on the observations of others (Caba-Vinagre, personal communication)
(g)-Total equals 112 because an exact time for 1 mating was not recorded
(h)-In seconds
(i)-In minutes
(j)-Listed according to descending dominance rank order
(k)-Niemeyer (1980), Niemeyer and Chamove (1983)

18 (66%) of 27 days herein, whereas Estep et al. (1984) reports multiple matings occurring on 20 (77%) of 26 days. These differences between studies may reflect differences in research settings with the confining circumstances of captivity possibly contributing to increased sexual activity.

With the matings themselves, the average pre- and post-ejaculatory durations in this study were 27.85 and 69.47 seconds respectively, with a mean overall duration of 97.32 seconds for each of the matings recorded. This compares with 35.5, 70.8 and 106.3 seconds for the pre- and post-ejaculatory and overall durations sited by Niemeyer (1980; Niemeyer and Chamove, 1983). Chevalier-Skolnikoff (1975) reported durations of 59, 114 and 168 seconds respectively, and Estep et al. (1984) reported 16.8 seconds for the pre-ejaculatory period, 88.8 seconds for the tie phase, and 105.6 seconds for an entire mating. Bruce (1984) reported a mean tie length of 85.8 seconds. Also, the mean number of minutes between multiple matings is 14.33 reported by Estep et al. (1984), compared with 19 minutes reported herein. Basically, then, variation in mating between all these studies, except that of Chevalier-Skolnikoff, seems to be relatively slight. The substantially higher durations reported by Chevalier-Skolnikoff may be attributed to the idiosyncratic nature of her particular subjects or to the low number of matings she recorded.

Individual

Estep et al. (1984) reported that, of the 2 adult males in their study group, the highest ranking monopolised all 146 (100%) matings recorded. The alpha male in the present study participated in 78 (75%) of 113 matings, and this same trend has also been reported by others (Estep et al., 1988; Niemeyer and Chamove, 1983; Gouzoules, 1974). In other words, for whatever reason(s), it is common for males of alpha status in stumptails

to do most of the mating. Among adult females, the distribution is not quite as skewed as for males, but mating is still not random. Estep et al. (1984) reported that of 7 mating females 3 accounted for 121 (83%) of the 146. This is quite similar to the present study where 4 of the 10 females observed mating participated in 85 (75.22%) of the 113 recorded, and, in both cases, it was unrelated to dominance. It may result from the mating preference of the alpha male.

Finally, before moving on to sexual interference in the next chapter, the associations of male and female age and parity on the frequency of mating can be compared. According to both Estep et al.(1984) and what was found in this study, all are unrelated.

CHAPTER 7

SEXUAL INTERFERENCE

This chapter will present the basic results on sexual interference from this study and then compare them with and discuss the differences of the three previous studies of interference in stumptails. But first, as an introduction, an explanation will be offered for why interference is distributed among primates as it is, particularly in stumptails. A brief description of interference among stumptails will also be outlined. The purpose of the chapter, like the last, is to provide background and data for theoretical discussion in Chapters 8 and 9.

DISTRIBUTION OF SEXUAL INTERFERENCE AMONG PRIMATES

According to Thierry (1986), the form and frequency of sexual interference in primates depends on the level of tolerance of adult males. For example, in species where agonistic interactions between individuals are basically symmetrical, even if imposed by coalition, interference during matings is often developed and relatively common. However, in species where agonistic asymmetry exists, sexual interference is less developed or frequent, or altogether nonexistent. If the chances are great of being seriously injured by sexually interfering in the matings of dominant and

aggressive males, the cost of doing so will probably outweigh the benefit of preventing them from mating (Clutton-Brock and Harvey, 1976; Bertram, 1976). But, is there more involved than just this? In reality, maybe a different question needs to be asked such as: what is the particular circumstance responsible for a species' specific level of agonism? To try and answer this question, a coefficient of relatedness between members of a species may be of greater importance. It is likely that the greater the genetic relatedness between group members, the less they will be agonistic toward each other, and the reverse: the less members are related, the more they will be agonistic. Therefore, rather than being based solely on agonism, the form and frequency of sexual interference for any given species may ultimately be dependent upon just how closely related its members within a population are. It is proposed, for primates, high species' relatedness, or high relatedness between same sexed individuals within a species, will serve to lower the amount and kind of sexual interference. However, if species or like sexed relatedness within a species is low, interference will be relatively high, although the upper level of this latter prediction may be tempered by high levels of dominant male agonism. Because of this, sexual interference among most species of primates should predictably occur at only very low to moderate levels. This is because, in the first instance, species members are too closely related for sexual interference to be beneficial (in an inclusive fitness sense), and, in the second instance, male agonism works to inhibit sexual interference. Therefore, in either closely related or highly agonistic populations, high levels of interference are much too costly to evolve. A similar proposal has been forwarded by Bertram (1976) to explain why within prides of lions adult males do not compete for oestrous females.

When reviewing the primate species listed in Chapter 2, it does appear

that sexual interference is more common among uni- and multimale breeders who are generally less close genetically than are monogamous breeders (see Table 7.1). But, even so, why are stumptails the only primate exception that shows an extremely high level of sexual interference (e.g., 83% of all matings according to the present study) if, as proposed, they should display only a moderate amount as do other minimally related multimale breeders? The answer, I suggest, lies with the tie.

In the last chapter, it was shown that male and female stumptails are unique in the morphology of their genitalia. Both sexes differ considerably from other species of primates. It was also shown that in one aspect of their copulatory pattern they differ as well: the genital tie. These two differences appear to be interdependent, but what may be even more important here is that sexual interference could also be associated. What is proposed is that without the genital tie the extremely high frequency of interference observed among stumptails may not exist, but may instead occur at the much lower rate noted for other multimale species. In other words, without the tie to help prevent an agonistic male from retaliating, interference may be too costly. But, since tying does exist among stumptails, at least hypothetically, so does a high level of sexual interference.

DESCRIPTION OF SEXUAL INTERFERENCE AMONG STUMPTAILS

As noted by Gouzoules (1974), sexual interference in stumptails rarely occurs before ejaculation, but it is common for various members of a group to begin orienting toward a pair just prior to their mating. In anticipation of mounting, they start by feigning indifference (Bertrand, 1969) until the exact moment of ejaculation, whereby they immediately rush toward the pair

TABLE 7.1. List of sexually interfering primate species reviewed in Chapter 2 according to their type of mating system or overall coefficient of relatedness.*@

MATING SYSTEM		
Multimale	Unimale	Monogamous
Ringtail Lemur	Common Langur	Common Marmoset
Brown Capuchin	Nilgiri Langur	Gibbon
Howler Monkey	Blue Monkey	
Squirrel Monkey	Sykes Monkey	
Spider Monkey	Patas Monkey	
Vervet Monkey	Gelada Baboon	
Red Colobus Monkey		
Grey-Cheeked Mangabey		
Japanese Macaque		
Rhesus Macaque		
Stumptail Macaque		
Crabeating Macaque		
Tonkean Macaque		
Bonnet Macaque		
Barbary Macaque		
Pigtail Macaque		
Crested Macaque		
Olive Baboon		
Yellow Baboon		
Chimpanzee		
Gorilla		

*=Bushbabys and orangutans are not listed because both are solitary breeders and, therefore, do not normally have group members available to interfere.

@=Mating systems according to Hrdy and Whitten, 1987.

and begin interfering (Figures 7.1-7.6). Based on personal observation, the motor patterns most often involved are rapid approaching and withdrawing, while staring at the male and teeth-chatter grimacing (Appendix). At an extreme, intruders may hit either of the pair, but more likely the male, before darting off. Upon returning, they continue interfering. The most mild form of interference is moving toward the pair and staring.

Responses of the mating pair to interference varies. The copulating male commonly threatens the intruders with an open mouth (Appendix) (Figures 7.5 and 7.6). Only rarely does he actually break the tie to retaliate against them. The usual response of the female is to remain passive until the mating comes to an end. Before it does, however, most, if not all, of the intruders have by then resumed their prior pre-interference activities.

RESULTS

Similar to the previous chapter, general interference data from this study will be presented first, followed by comparisons with the results of others.

Group

Of the 113 matings recorded, 94 (83%) received sexual interference (Figure 7.7). This resulted in 395 cases of intrusion involving 47(81%) individuals. Of these 47, 16 (34%) were males and 31(66%) were females (Figure 7.8). Furthermore, in the 94 (83%) matings receiving interference, the average number of intruding individuals for each mating was 4.2 (range: 1-18). This is reflected in Figure 7.9. As can be seen, just over half (55%, N=62) of the matings had from 1 to 4 intruders, while matings with 13-16 intruders never occurred. Finally, the mean number of intrusions for each of the 47 individuals who interfered was 8.4 (range: 1-33).

FIGURE 7.1. McGregor mating with Rosy.

FIGURE 7.2. McGregor with a frown-round-mouth expression which signals ejaculation. Interference begins.

FIGURE 7.3. McGregor tied, sitting back, and threatening an intruder, while interference (mild in this case) continues by the individual in the foreground.

FIGURE 7.4. Rosy and McGregor remain tied. McGregor continues threatening.

FIGURE 7.5. Tying and threatening continue.

FIGURE 7.6. McGregor stands and continues threatening.

FIGURE 7.7. Percent of matings receiving sexual interference.

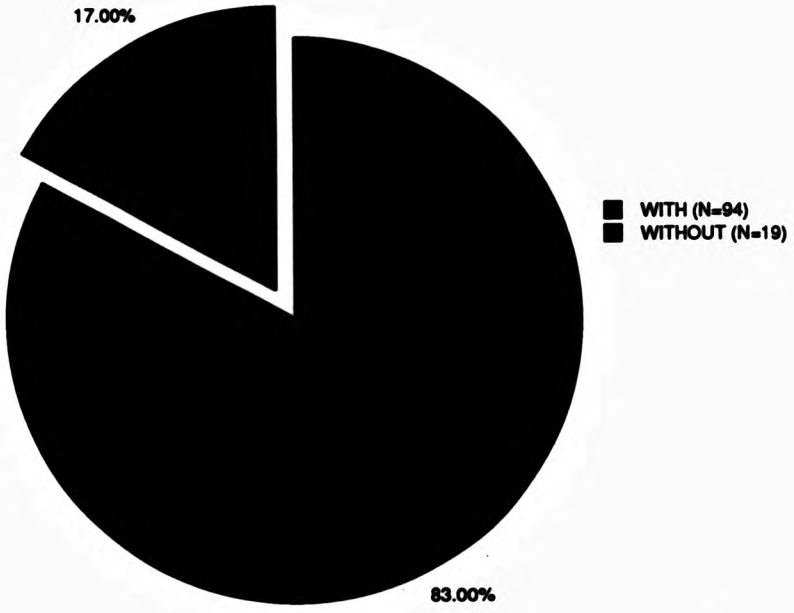


FIGURE 7.8. Percent of individuals interfering by sex.

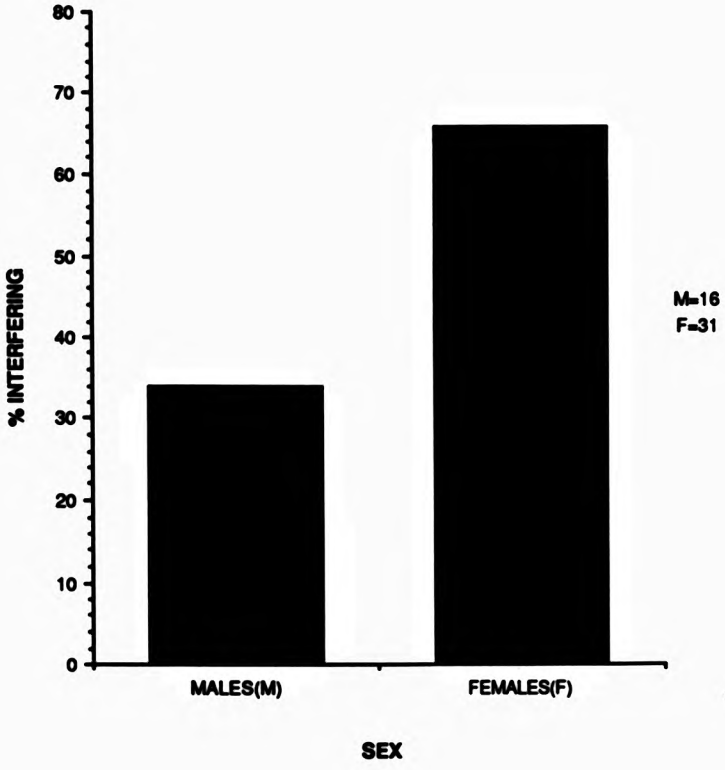
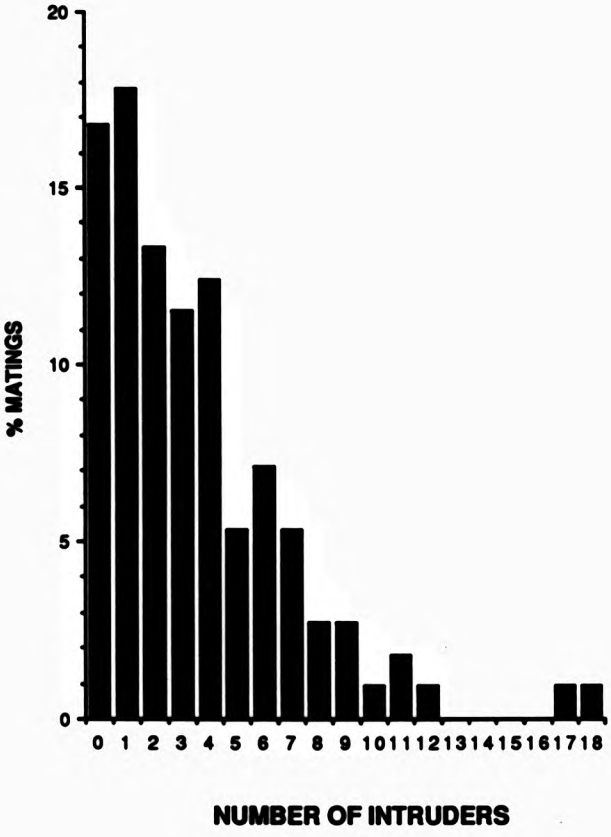


FIGURE 7.9. Percentages of matings by number of intruders.



Interference was directed most often to the male. For example, of the one-zero instances (Chapter 4) where either the mating male or female were actually hit or grabbed (Appendix), the times the male was contacted out-numbered the female by almost 2 to 1 (N=11 and N=6, respectively). Also, the male was unsuccessfully hit or grabbed at 6 times, whereas this never happened to the female.

When considering interruptions, interference was never observed to prevent a mating, but on 3 (3%) occasions a mating male (twice by Pancho and once by McGregor) did terminate the tie phase early to retaliate against particular intruders (Ucilia and Jarocha, and Mario, respectively). Also, the number of instances whereby an intruder chased another active intruder was three.

Individual

As described in Chapter 4, a combined score was developed to measure intensity for each case of intrusion. These scores were then totalled for each of the 47 individuals who sexually interfered. This provided the simplest method to distinguish between subjects. As can be seen from Table 7.2, the differences were vast. Listed in descending order, the scores range from a high of 15805 to a low of 72.

When the scores were grouped by sex, even though the total for females out-numbered that of males [because there were more females than males in the group (16 compared to 31)], males ended up providing 64%(N=113733.76) of all the sexual interference observed (Figure 7.10). Females contributed 36%(N=63975.24). This difference was highly significant (Mann-Whitney U test, z=-2.40, p=.017, 2-tailed).

TABLE 7.2 Degree of sexual interference for each individual subject. Listed in descending order.

Intruder	Age-Sex Group	Combined Score	Frequency	Percent
Ucilia	SA-F	15805	28	8.89
Blair	SA-M	14902	33	8.39
Pierre	A-F	14619	23	8.23
Mario	SA-M	13079	30	7.36
Flavia	SA-F	8833	19	4.98
Bruto	SA-M	8543	22	4.81
Chimuelo	A-M	7781	19	4.38
Flan	SA-M	7724	20	4.34
Santos	SA-M	7355	16	4.13
Lorenzo	SA-M	7036	13	3.96
Elena	A-F	6973	9	3.92
Canela	A-F	6644	14	3.74
Bruno	SA-M	5257	10	2.96
Fanny	A-F	4942	11	2.79
Roberto	SA-M	3891	9	2.19
Mirna	A-F	3690	9	2.08
Flaca	A-F	3521	10	1.98
Enriqueta	SA-F	3196	7	1.80
Brisa	J-F	3034	5	1.71
Lupita	I-F	2846	9	1.60
Marcela	SA-F	2757	7	1.56
Negra	A-F	2754	5	1.54
Florinda	I-F	2492	7	1.40
Wilfrido	SA-M	2164	5	1.22
Florencio	J-M	2086	4	1.17
Jobo	A-M	1720	6	.97
Blasita	SA-F	1585	5	.89
McGregor	A-M	1399	5	.79
Piedad	J-F	1196	4	.68
Miguelito	J-M	1187	4	.66
Rosy	A-F	1008	2	.57
Bruja	A-F	999	3	.56
Sigri	SA-F	859	3	.48
Luciano	A-M	750	1	.42
Juanita	A-F	729	2	.41
Blas	J-M	674	2	.38
Jarocha	A-F	607	2	.34
Elpidia	J-F	567	1	.32
Flossie	SA-F	520	1	.29
Blondie	A-F	410	1	.23
Blanca	A-F	410	1	.23
Martha	SA-F	336	1	.19
Teresa	A-F	240	1	.14
Lucia	A-F	217	2	.12
Rosa	J-F	204	1	.11
Blonny	I-F	96	1	.05
Lolita	A-F	72	2	.04
Miriam	SA-F	00	0	.00
Lourdes	I-F	00	0	.00
Blenda	I-F	00	0	.00
Julieta	I-F	00	0	.00
J.D.	A-M	00	0	.00
Pancho	A-M	00	0	.00
Tigre	A-M	00	0	.00
Teo	I-M	00	0	.00
Millo	I-M	00	0	.00
Martin	I-M	00	0	.00
Ernesto	I-M	00	0	.00
TOTAL:	58	177709	395	100.00

FIGURE 7.10. Percent of sexual interference by sex. Weighted by mean scores.

The difference in amount of interference between age and sex subcategories was also significant (Kruskall-Wallis test, $H(7)=12.98$, $p<.05$). Infant males were not observed to interfere at all, but, of the 7 other age/sex groups, subadult males contributed the most with 34.88% of the total. Subadult females interfered at the second highest level contributing 19%, followed by adult females with 13.41%, adult males with 13.07%, infant females with 8.13%, juvenile males with 5.9%, and juvenile females with 5.61% (Figure 7.11).

Concerning interference by matriline, even though Flaca's provided 24.15% (Figure 7.12), the differences between this and the others were not significant (Kruskall-Wallis test, $H(7)=6.49$, $p>.05$).

Other variables were also tested to determine which individuals interfered. However, interference was not significantly correlated with the rank of the intruder (Spearman rank correlation coefficient test, $r_s=.26$, $p=>.05$) (Table 7.3), the degree of affiliation the intruder had with the mating male or female (median scores of $r_s=.244$, $p>.05$ and $r_s=.026$, $p>.05$, respectively) (Tables 7.4 and 7.5), or the intruders' coefficient of relatedness with the mating female (median correlation of $r_s=.192$, $p>.05$) (Table 7.6). It should be noted though that with two of the mating females, Flaca and Bruja, interference was positively correlated with both the amount of intruder affiliation ($r_s=.556$, $p=.016$ and $r_s=.402$, $p=.049$, respectively) and the degree of intruder relatedness ($r_s=.604$, $p=.004$ and $r_s=.541$, $p=.019$, respectively). In the latter instance, this may have been because juvenile and infant interference was also positively correlated with female relatedness ($r_s=.266$, $p=.034$ and $r_s=.378$, $p=.009$, respectively). In addition, sexual interference was positively correlated with the dominance

FIGURE 7.11. Percent of sexual interference by age/sex group. Weighted by mean scores.

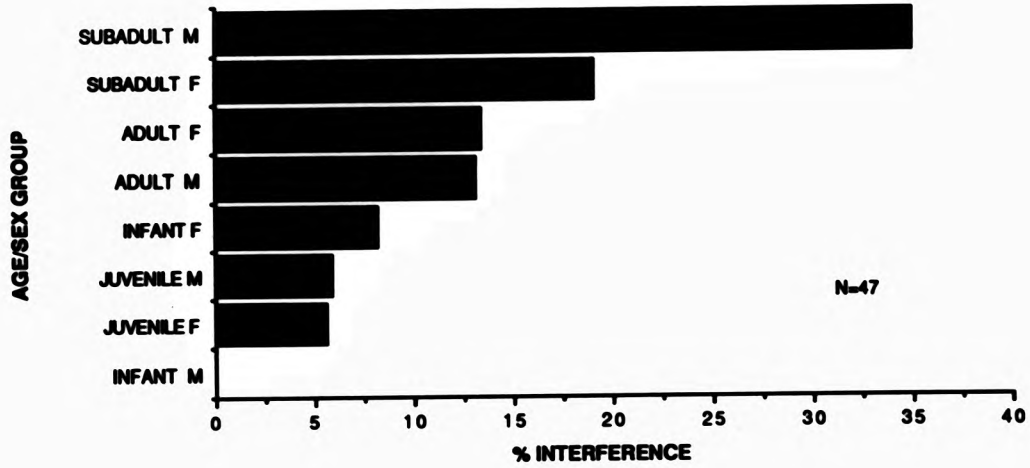


FIGURE 7.12. Percent of sexual interference by matriline. Listed by dominance rank order. Weighted by mean scores. McGregor was not included for lack of matriline affiliation.

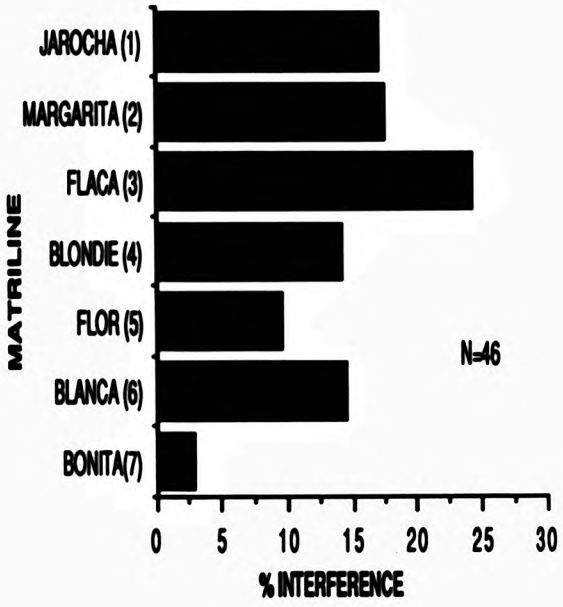


TABLE 7.3 Dominance rank order matrix. Determined by dyadic agonistic encounters.

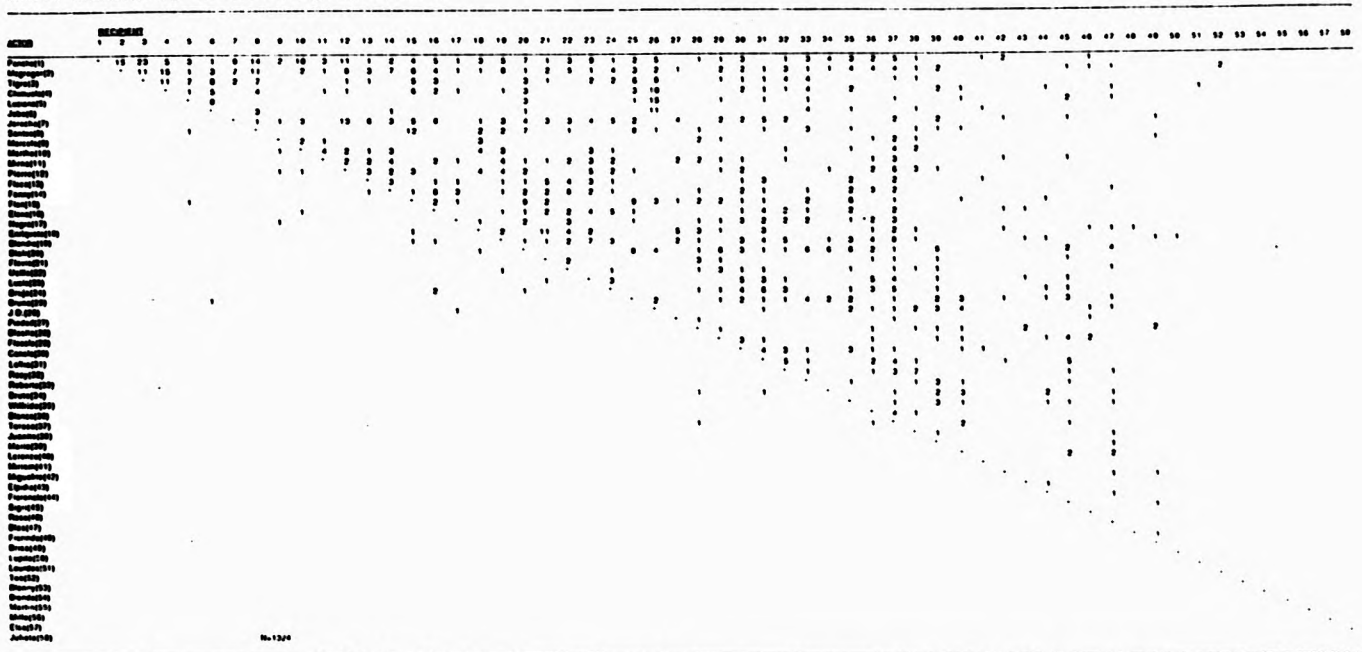


TABLE 7.4. Intruder's affiliation (in seconds) with mating female. Females listed by dominance rank order, intruders by descending order of combined score.

	FEMALE								
INTRUDER	Pierre	Flaca	Fanny	Elena	Ucilia*	Lucia	Bruja	Flossie	Canela	Rosy
Ucilia	202	2844	1290	3155		245	89	1718	0	395
Blair	112	158	0	0		178	213	107	549	96
Pierre	-	556	0	389		541	81	529	151	378
Mario	0	824	17	0		18	92	1200	76	0
Flavia	58	4086	1303	620		76	228	816	105	349
Bruto	1319	0	245	0		343	1821	101	0	206
Chimuelo	735	252	45	480		766	635	15	127	600
Flan	24	1406	681	100		360	322	90	48	494
Santos	1503	149	43	0		0	83	414	176	30
Lorenzo	0	292	0	0		0	0	0	395	160
Elena	79	2211	941	-		784	0	2518	116	1420
Canela	553	112	0	1348		135	709	3489	-	147
Bruno	86	0	69	83		0	1803	424	255	13
Fanny	233	3079	-	902		21	117	1481	9	268
Roberto	0	0	0	0		0	0	112	0	127
Mirna	2777	658	0	810		1704	32	1680	15	52
Flaca	425	-	974	908		152	0	1485	309	431
Enriqueta	2967	395	16	657		636	249	567	0	660
Brisa	570	30	310	0		4054	5738	56	12	27
Lupita	1563	542	202	69		5134	1403	38	10	0
Marcela	2600	638	160	0		800	0	18	151	48
Negra	351	3052	1103	2058		1012	106	1403	789	692
Florinda	361	6688	539	73		313	177	1364	609	349
Wilfrido	0	0	0	205		0	0	1150	248	29
Florencio	247	196	0	753		156	0	2454	1793	0
Jobo	16	144	0	5		0	366	258	285	34
Blasita	427	979	582	17		1953	1190	0	330	0
McGregor	180	1014	959	120		1200	3386	1270	211	728
Piedad	3382	0	271	479		0	0	508	151	0
Miguelito	1427	146	57	798		0	0	508	0	0
Rosy	0	0	544	475		23	568	798	373	-
Bruja	717	64	424	0		3288	-	412	568	70
Sigri	0	395	22	110		184	390	802	691	2200
Luciano	0	0	0	0		491	14	96	845	569
Juanita	0	460	365	370		93	26	0	409	102
Blas	56	146	957	0		749	0	600	44	0
Jarocha	2760	1200	17	1276		112	14	1262	651	788
Elpidia	217	1460	67	4146		267	0	1708	11	346
Flossie	0	196	58	1879		495	172	-	3828	660
Blondie	1310	1661	138	438		3629	1516	820	1397	78
Blanca	938	2417	324	39		2696	832	497	74	167
Martha	4251	760	99	428		1973	40	577	0	53
Teresa	1797	1292	0	600		1808	377	1697	800	478
Lucia	1464	493	153	51		-	1657	1046	612	74
Rosa	0	151	259	34		0	0	154	0	1847
Blonny	1109	1171	165	340		1966	773	617	1056	11
Lolita	113	146	50	617		0	1225	771	372	1649

* Untested

NOTE: Underlining represents mother/immature offspring (selected according to mother mating/immature offspring interfering)

TABLE 7.5. Intruder's affiliation (in seconds) with mating male. Males listed by dominance rank order, intruders by descending order of combined score.

	MALE							
INTRUDER	Pancho	Mcgregor	Tigre	Chimuelo	Jobo	Flan	Bruno	Roberto
Ucilia	595	2587	427	277	627	1112	223	0
Blair	188	607	78	26	118	210	1686	724
Pierre	1770	44	47	71	24	470	106	0
Mario	178	263	289	50	0	529	259	21
Flavia	202	351	0	48	0	3340	49	0
Bruto	44	440	21	639	58	713	4155	55
Chimuelo	98	0	426	-	168	325	218	1200
Flan	125	68	518	395	9	-	33	25
Santos	1126	0	218	66	551	618	161	19
Lorenzo	240	100	0	52	730	429	155	1021
Elena	824	1773	0	7	667	1091	0	0
Canela	600	638	136	22	893	248	115	227
Bruno	148	386	290	762	600	123	-	390
Fanny	175	470	559	99	83	1667	23	50
Roberto	0	25	553	481	1487	0	0	-
Mirna	1892	600	826	94	0	26	0	0
Flaca	204	351	55	0	0	821	36	0
Enriqueta	72	0	299	70	0	90	5	8
Brisa	245	1205	0	206	0	607	54	0
Lupita	273	109	623	12	0	600	28	0
Marcela	672	642	137	0	0	89	0	0
Negra	70	1354	0	0	61	1307	15	416
Florinda	145	1509	47	0	0	1334	0	0
Wilfrido	1230	54	23	0	0	228	24	841
Florencio	600	48	159	14	0	106	75	199
Jobo	33	33	161	0	-	28	456	1114
Blasita	303	1102	0	50	0	498	0	0
McGregor	227	-	7	10	104	816	61	34
Piedad	1057	223	406	0	0	67	0	0
Miguelito	11	0	484	18	11	424	1491	0
Rosy	233	0	370	600	96	80	0	168
Bruja	0	3166	0	341	83	600	390	116
Sigri	0	351	0	1066	310	24	49	581
Luciano	0	0	0	0	118	0	786	303
Juanita	38	1377	237	217	0	165	806	351
Blas	35	0	67	671	189	982	216	144
Jarocha	350	106	3061	988	0	800	0	577
Elpidia	840	977	140	601	845	1391	21	41
Flossie	632	351	118	0	828	302	596	16
Blondie	1031	849	71	325	115	1078	0	0
Blanca	671	1374	226	16	419	635	326	0
Martha	999	211	780	47	188	775	0	0
Teresa	493	2266	989	7	27	1155	167	66
Lucia	514	119	600	13	0	703	313	0
Rosa	0	0	0	36	0	0	0	168
Blonny	716	722	491	110	42	623	0	0
Lolita	0	73	176	944	200	72	0	893

TABLE 7.6. Intruder's coefficient of relatedness(r) with mating female. Females listed by dominance rank order, intruders by descending order of combined score.*

INTRUDER	FEMALE Pierre	Flaca	Fanny	Elena●	Ucilia●	Lucia	Bruja	Flossie●	Canela	Rosy
Ucilia	0	.250	.125			0	0		0	0
Blair	0	0	0			.250	.250		0	0
Pierre	-	0	0			0	0		0	0
Mario	0	0	0			0	0		0	0
Flavia	0	.500	.250			0	0		0	0
Bruto	0	0	0			.125	.500		0	0
Chimuelo	0	0	0			0	0		0	0
Flan	0	.500	.250			0	0		0	0
Santos	.500	0	0			0	0		0	0
Lorenzo	0	0	0			0	0		.125	.125
Elena	0	.500	.250			0	0		0	0
Canela	0	0	0			0	0		-	.250
Bruno	0	0	0			.125	.500		0	0
Fanny	0	.500	-			0	0		0	0
Roberto	0	0	0			0	0		.125	.500
Mirna	.250	0	0			0	0		0	0
Flaca	0	-	.500			0	0		0	0
Enriqueta	.500	0	0			0	0		0	0
Brisa	0	0	0			.125	.500		0	0
Lupita	0	0	0			.500	.125		0	0
Marcela	.250	0	0			0	0		0	0
Negra	0	.500	.250			0	0		0	0
Florinda	0	.500	.250			0	0		0	0
Wilfrido	0	0	0			0	0		.250	.250
Florencio	0	0	0			0	0		.250	.250
Jobo	0	0	0			0	0		.250	.250
Blasita	0	0	0			.250	.250		0	0
McGregor	0	0	0			0	0		0	0
Piedad	.500	0	0			0	0		0	0
Miguelito	.125	0	0			0	0		0	0
Rosy	0	0	0			0	0		.250	0
Bruja	0	0	0			.500	-		0	0
Sigrl	0	0	0			0	0		.125	.500
Luciano	0	0	0			.250	.250		0	0
Juanita	0	0	0			0	0		0	0
Blas	0	0	0			0	0		0	0
Jarocha	0	0	0			0	0		0	0
Elpidia	0	.250	.125			0	0		0	0
Flossie	0	0	0			0	0		.250	.250
Blondie	0	0	0			.500	.500		0	0
Blanca	0	0	0			0	0		0	0
Martha	.250	0	0			0	0		0	0
Teresa	0	0	0			0	0		0	0
Lucia	0	0	0			-	.250		0	0
Rosa	0	0	0			0	0		.125	.500
Blonny	0	0	0			.250	.250		0	0
Lolita	0	0	0			0	0		.250	.250

* Scores represent minimum relatedness

● Mated without interference

rank order of the mating male (r_s=1.00, p<.001), but not with the dominance rank of the mating female (r_s=.036, p>.05). Finally, interference was not correlated with the age of either the mating male or female (r_s=1.00, p=.500 and r_s=.143, p>.05, respectively).

COMPARISONS AND DISCUSSION

What follows is comparison of the above findings with those of other studies (see Table 7.7 for a summary). As with the socio-sexual results, any differences may be attributed to the variation among research settings, the most naturalistic being represented by Tanaxpillo. Another possibility is that the differences may be attributed to the variation of measures used between studies.

Group

As noted in more detail in Chapter 2, only three projects (all in captivity) have studied sexual interference among stumptails previous to the present project. These were by Gouzoules (1974), Niemeyer (1980, Niemeyer and Chamove, 1983), and Bruce (1982, 1984). Like this study, all three recorded high percentages of sexual interference. In the Gouzoules study, 81% (N=79) of the matings received interference, while 93%(N=252) of the matings were intruded upon in the study by Niemeyer, and 89%(N=618) in Bruce's study. Eighty-three percent (N=94) of the matings in this study included interference, and the slightly reduced level may be due to the lack of forced proximity found in captivity, even though Gouzoules found a reduced level as well.

Also similar between projects is the number of intruding individuals per

TABLE 7.7 Results summary of sexual interference in *Macaca arctoides.*

Behaviour	SOURCES			
	Brereton (this study)	Gouzoules('74)	Niemeyer('80, Niemeyer and Chamove, '83)	Bruce('82, '84)
GROUP				
Mating with Interference	83%(N=94)	81%(N=79)	93%(N=252)	89%(N=618)
Cases of Interference	395	-	-	-
Subject's Interfering	47 of 58	14 of 19	22 of 22	range:15-24
Male	34%(N=16)	36%(N=5)	27%(N=6)	-
Female	66%(N=31)	64%(N=9)	73%(N=16)	-
Intruders per Mating	4.2 (range:1-18)	Maximum:9	-	-
Intrusions per Individual	8.4 (range:1-33)	-	-	-
Matings by Intruder Number	16.8%- 0 17.8%- 1 13.3%- 2 11.5%- 3 12.4%- 4 5.3%- 5 7.1%- 6 5.3%- 7 2.7%- 8 2.7%- 9 .9%-10 1.8%-11 .9%-12 0%-13 0%-14 0%-15 0%-16 .9%-17 .9%-18	-	-	-
Interference to Mating Pair (Hit or Grabbed and Hit or Grabbed At)	Male-11/6 Female-6/0	Male	Male	Male

TABLE 7.7. Continued.

Behaviour	SOURCES			
	Brereton (this study)	Gouzoules('74)	Niemeyer('80, Niemeyer and Chamove, '83)	Bruce('82, '84)
Cases of Intruder Chasing Another Intruder	3	-	17	-
Matings Interrupted by Interference	0	5	?	0
Matings Terminated Early for Retaliation	3	0	?	-
INDIVIDUAL				
Combined Score(b) by Individual	Ucilia-15805 Blair-14902 Pierre-14619 Mario-13079 Flavia-8833 Bruto-8543 Chimuelo-7781 Flan-7724 Santos-7355 Lorenzo-7036 Elena-6973 Canela-6644 Bruno-5257 Fanny-4942 Roberto-3891 Mirna-3690 Flaca-3521 Enriqueta-3196 Brisa-3034 Lupita-2846 Marcela-2757 Negra-2754 Florinda-2492 Wilfrido-2164 Florencio-2086	-	-	-

-continued-

TABLE 7.7. Continued.

Behaviour	SOURCES			
	Brereton (this study)	Gouzoules('74)	Niemeyer('80, Niemeyer and Chamove, '83)	Bruce('82, '84)
	Jobo-1720 Blasita-1585 McGregor-1399 Piedad-1196 Miguelito-1187 Rosy-1008 Bruja-999 Sigri-859 Luciano-750 Juanita-729 Blas-674 Jarocha-607 Elpidia-567 Flossie-520 Blondie-410(a) Blanca-410(a) Martha-336 Teresa-240 Lucia-217 Rosa-204 Blonny-96 Lolita-72			
Combined Score by Sex	Males-64% (N=113733.76) Females-36% (N=63975.24)	No Difference	No Difference	Females Interfere More Than Males
Combined Score by Age/Sex	SA-M=34.88% SA-F=19% A-F=13.41% A-M=13.07% I-F=8.13% J-M=5.9% J-F=5.61% I-M=0	Subadult and Juvenile Males and Females Interfere More Actively	Young Adult Females-51%(of Matings) Infant Females-43% Young Adult Males-31% Infant Males-27% Adult Females-20% Adult Males-12%	No Difference
Combined Score by Matriline(c)	Jarocha-17% Margarita-17.4% Flaca-24.15% Blondie-14.24% Flor-9.66% Blanca-14.6% Bonita-2.95%	-	-	-
Correlation: Interference with Dominance Rank (Intruder)	No	-	Yes	No

TABLE 7.7. Continued.

Behaviour	SOURCES			
	Brereton (this study)	Gouzoules('74)	Niemeyer('80, Niemeyer and Chamove, '83)	Bruce('82, '84)
Correlation: Interference with Affiliation (Intruder/Mating Male)	No (Overall)	-	No	-
Correlation: Interference with Affiliation (Intruder/Mating Female)(d)	No (Overall)	-	Yes	-
Correlation: Interference with Relatedness (Intruder/Mating Female)(d)	No (Overall)	No	Yes	No
	Yes (Juven./Inf.)	No	Yes	No
Correlation: Interference with Dominance Rank (Mating Male)	Yes	No	Yes	Yes
Correlation: Interference with Dominance Rank (Mating Female)	No	Yes	Yes	Yes
Correlation: Interference with Age (Mating Male)	No	-	Yes	Yes
Correlation: Interference with Age (Mating Female)	No	-	Yes	-

*=Numbers either equal raw data or means, the difference is self-evident; percent is specified
?=Unknown
a=Tie score
b=Calculation: One-zero intruder behaviour + one-zero retaliatory behaviour + one-zero response behaviour x intruder duration, totalled
c=Listed by descending dominance rank order
d=Yes for Flaca and Bruja

population. In this study, out of the total of 58 subjects, 47 (81%) were observed to interfere at least once. Sixteen of these individuals were males and 31 were females. Gouzoules found that out of 19 subjects, 14 (74%) intruded. In his group, 5 of the 14 were males and 9 females. For Niemeyer, of the 22 subjects, all (100%) of them interfered over the course of her study. Six were males, and 16 were females. It is unknown just how many individuals were involved in Bruce's study, but her subjects ranged in number from 15 to 24.

The average number of intruders present at each mating varied as well, and for this study it was 4.2 (range: 1-18). A mean score was not provided by Niemeyer, and Gouzoules only mentions a maximum of 9. Bruce broke the average down by the rank of individual males, but, like Niemeyer, did not provide an overall figure.

The different studies also found some trends, although minimal variation in behaviour seems to exist. As to which of the mating individuals interference is most often directed, all four studies found the mating male to be the primary focus. In addition, this study found that, besides focusing on the pair, an intruder also chased another intruder 3 times. This occurred 17 times in the Niemeyer study. Furthermore, interference was never observed to prevent mating in this or the Bruce study, although it did in the studies of Gouzoules (N=5) and Niemeyer (number unknown). Bruce did mention, however, that tie durations were shortened in some matings by more dominant males interfering. Similarly, Gouzoules never witnessed a male terminate his mating sequence early for purposes of retaliation, whereas in this study it was observed on 3 occasions. It was also witnessed by Niemeyer, but she did not say how often. Bruce does not mention it at all.

Individual

When sexual interference is broken down by sex, in this study males were discovered to interfere significantly more than females (64% compared with 36%). Bruce, on the other hand, found just the reverse: females interfere more than males. Both Gouzoules and Niemeyer mentioned that no significant differences exist between the sexes. It is not exactly certain why these differences exist between studies, but since the measures used to determine interference by sex differ considerably, this may be the explanation.

For the subcategories of age and sex, Bruce found no significant differences between the groups, whereas this study found subadult males (at 34.88%) interfering far beyond any of the other subgroups. The next highest was subadult females at 19%. This also differs from Niemeyer's findings. She discovered that young adult females (51% of matings) interfered the most, followed in descending order by infant females (43%), young adult males (31%), infant males (27%), adult females (20%), and adult males (12%). Gouzoules only mentions that subadult and juvenile males and females are more active interferers. Again, a simple explanation for these differences is not immediately obvious. However, it is suspected that the different ways interference was measured in each study may be the reason. Bruce and Gouzoules do not state their criteria for categorizing the amount of interference by age/sex subgroups, and Niemeyer appears to simply use the criteria of interfering of not interfering at matings. This could make a difference in interpretation. The age criteria for placing subjects in specific subgroups may also be responsible. Only Niemeyer and this study specify what these criteria are, and they both differ.

Concerning correlations with other variables, this study found no significant association between interference and dominance rank order,

between interference and affiliation with either of the mating pair, or between interference and relatedness with the mating female. Relatedness was, however, associated with juvenile and infant interference. Bruce also states that both dominance rank and relatedness were not correlated with interference, as was the case with relatedness in the Gouzoules study. This is all quite similar. Niemeyer, however, found something different. In her study, sexual interference was significantly correlated with both dominance rank and relatedness, and also affiliation with the mating female. Only interference and affiliation with the mating male was not positively correlated. The exact reasons for these differences between the Niemeyer study and the others are unknown, but the small area (54.28 m^3) to which her subjects were confined may be responsible. In other words, individuals of high rank could seldom be absent when matings occurred because of the small enclosure, nor could individuals of close relationship or affiliation. So it seems reasonable that in the Niemeyer study these variables could have had an influence on the amount and kind of interference.

Furthermore, all four studies found a correlation between interference and the dominance rank of the mating male or female. In this study, it was the rank of the mating male that determined the amount of interference the pair received, and not the rank of the female. In the Gouzoules study, however, it was the rank of the female that was important, rather than that of the male. Both Niemeyer and Bruce found that the amount of interference increased when either the mating male or female were of higher rank. This is similar, but different, and the reason may stem from the idiosyncratic nature of the subjects involved.

And finally, as to age, Niemeyer discovered that the matings of fully adult individuals received a greater degree of interference than did the matings of young adults. This was also the case with adult males in

Bruce's study, but interference and age were not correlated for either males or females in the present study. The differences here may again be from variations between studies in age subgroup criteria.

In summary, even though some differences between studies do exist, they can probably be explained by research setting, individual differences between subjects, methodology, or all three. But regardless of the exact reasons for these differences, an attempt should be made to describe an evolutionary framework for sexual interference in stumptail macaques because, in this species, interference is extraordinarily prominent. The remaining chapters will make an effort to do just this, even though it should be make clear that the approach taken is not the only approach possible, or even the correct one. But it is a holistic and evolutionary start which needs doing.

CHAPTER 8

SEXUAL INTERFERENCE: AS SPITE?

The primary goal of this chapter is to try to explain the ultimate function of sexual interference in stumptail macaques. The attempt is part of, continues through, and concludes in the next chapter. Before starting this task, however, relevant background information will be presented to place the suggested explanation in proper context. First, previously developed hypotheses will be briefly addressed, followed by a review of the possible effects of stress on reproduction, and then more results and the birth data from Tanaxpillo.

PREVIOUS HYPOTHESES

Explanations of behaviour within ethology are basically divided into one of two causes: proximate (motivational) or ultimate (functional). The difference between the two is one of time, and both are actually complimentary. Proximate causation is concerned with the specific mechanisms immediately responsible for a behaviour which, in turn, promotes the ultimate cause of adaptive significance through successful reproduction. Both address the question of why, but on different levels (Daly and Wilson, 1983).

For sexual interference in primates, hypotheses of both types have been

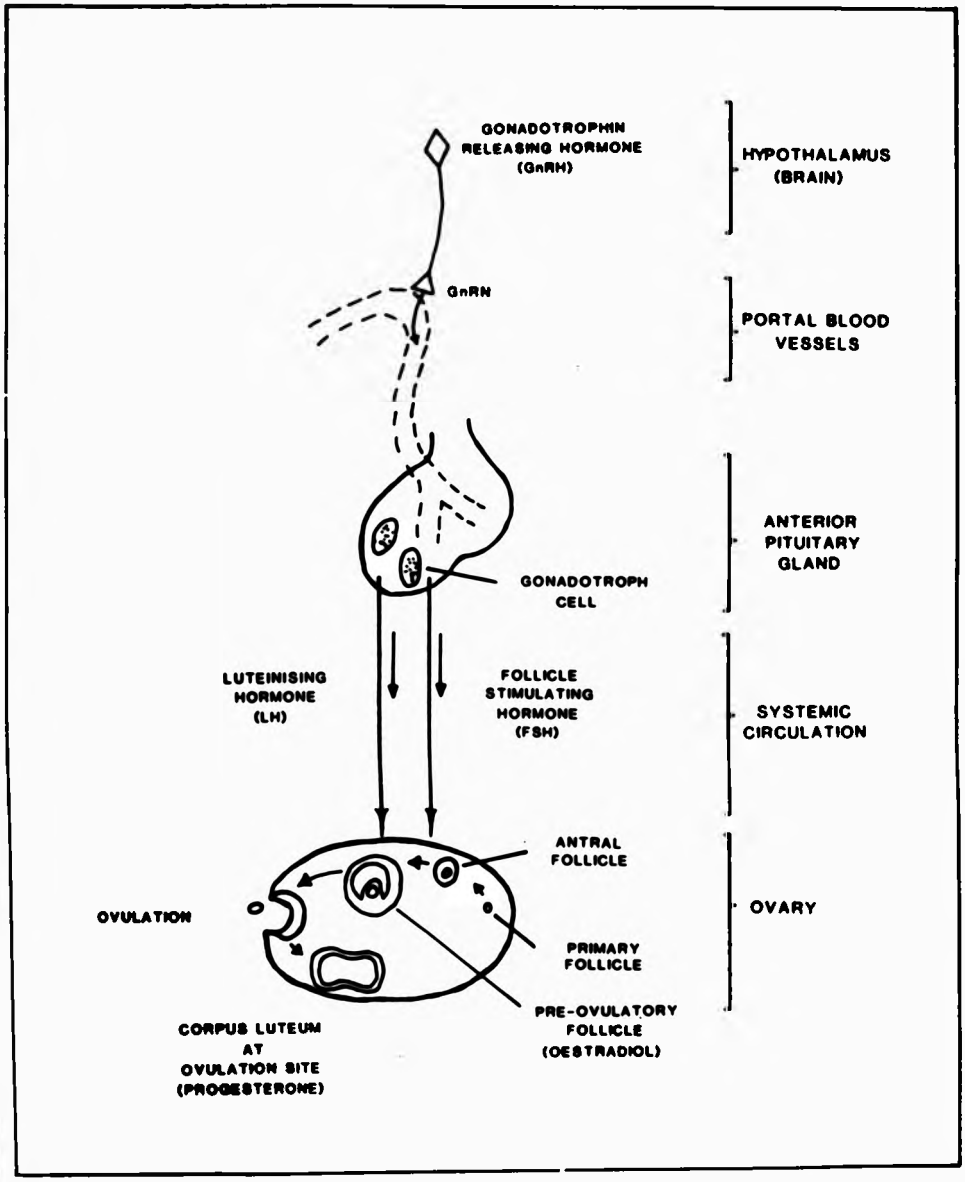
offered by previous authors. At the proximate level, its cause has been attributed to such things as the excitatory effect of observing matings (Loy and Loy, 1977; de Benedictis, 1973; Thierry, 1986; Zucker and Kaplan, 1981), the approach-avoidance conflict of being near dominant males (Loy and Loy, 1977; Rowell, 1967), observational learning of socio-sexual behaviour (de Benedictis, 1973; Hanby and Brown, 1974; Hess, 1973; Rowell, 1967; Struksaker, 1967a), and possessiveness of mating females (Niemeyer, 1980; Niemeyer and Chamove, 1983; Tutin, 1979). Of these, only this last explanation was applied to stumptails. According to the present free-ranging study, which found that interference was not associated with either relatedness or affiliation (Chapter 7), the possessiveness hypothesis is unlikely. More importantly, explanations at the ultimate level include intrasexual competition among adult males and females (Niemeyer, 1980; Niemeyer and Chamove, 1983; Bruce, 1984; Tutin, 1979; DeVore, 1965; Hall and DeVore, 1965; Harcourt et al., 1980; Hrdy, 1977; Stephenson, 1975; Struksaker, 1975), dominance/fitness testing of adult males (Loy and Loy, 1977; Bruce, 1984; Niemeyer, 1980; Niemeyer and Chamove, 1983; Zucker and Kaplan, 1981), and competition for future environmental resources (Hrdy, 1977). Again, only the first explanation of intrasexual competition was applied to stumptails, and Niemeyer and Bruce who propose it do not explain exactly how this would succeed since interference occurs after ejaculation. Also, in this free-ranging study, interference did not interrupt mating. This hypothesis will be expanded and considered in detail below. Other hypotheses at the ultimate level are the strengthening of bonds of affiliation between allies (Thierry, 1986), protection of the mating female from the mating male (Gouzoules, 1974), and parent-offspring conflict (Gore, 1986; Tutin, 1979; Rothe, 1975; Young, 1981). The protection of the mating female

from the mating male hypothesis, the only of this group applied to stumptails, was not supported by Niemeyer's captive study, nor is it qualitatively supported by the present free-ranging study. So, what potentially can explain the phenomenon of sexual interference in stumptail macaques? Based on the intrasexual competition hypothesis sighted above, the approach suggested here as worth pursuing is the possibility that sexual interference, even if directed at the male, might stress the mating pair enough to prevent, or at the very least, delay conception in the female. The remainder of this chapter will focus and discussion will be based on this hypothesis, starting with a brief review of how stress can effect reproduction in other primates.

EFFECTS OF STRESS ON REPRODUCTION

Even though there is some variation between species, in the ovarian cycle of female primates, hormones play an important and decisive role (Hodges, 1987). According to Abbott (1987) (Figure 8.1), it is gonadotrophin releasing hormone (GnRH) that starts the cycle in motion. Released from the hypothalamus at the base of the brain, GnRH drains through the portal blood vessels into the anterior pituitary gland where it "...stimulates the synthesis and release of LH [luteinising hormone] and FSH [follicle stimulating hormone] from gonadotroph cells into the blood stream" (Abbott, 1987:459). After being transported to the ovaries, LH and mostly FSH, stimulate follicular development. At this stage, "oestradiol secreted from the pre-ovulatory follicles initiates a massive discharge of LH which causes ovulation" (Abbott, 1987:459). After ovulation, progesterone producing corpus luteum is formed from the remaining follicular tissue. This serves to stimulate implantation and the

FIGURE 8.1. The role of hormones in female primate ovulation (from Abbott, 1987). See text for explanation.



maintenance of early pregnancy. If pregnancy does not result, the corpus luteum simply degenerates and another is not formed until a new cycle begins (Abbott, 1987). This process is considered normal in primates.

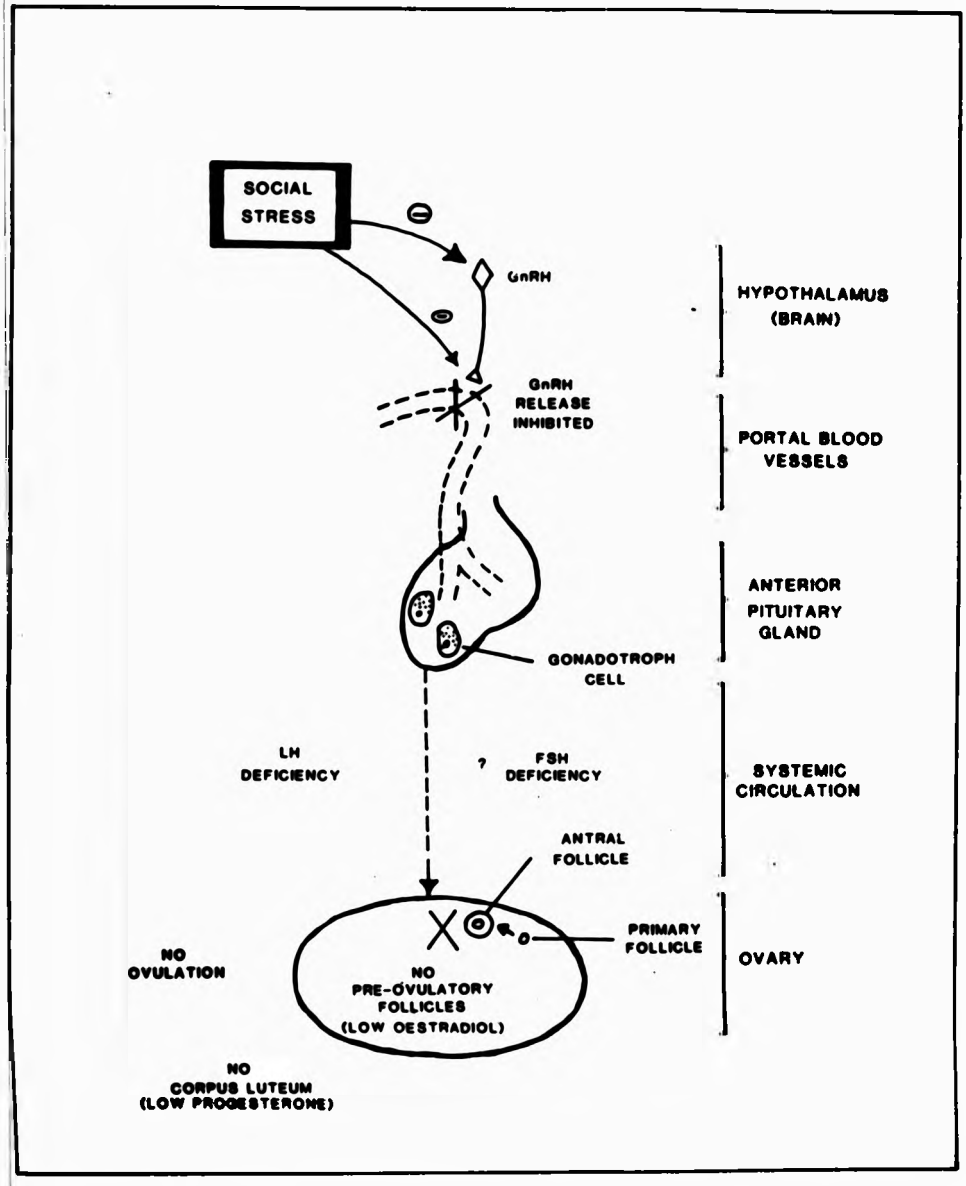
What is normal, however, is not always what occurs. Over the past decade, various researchers have discovered that, among other causes, social stress can significantly alter a female primate's ovarian cycle (see Table 8.1). When psychological stress is experienced, the female's brain is programmed to respond by immediately pumping endogenous opiates, enkephalins, and endorphins into the blood stream (Dunbar, 1988). This dampens the discomfort long enough to escape from the source. The process is identical for physical injury. One of the by-products of having opiates in the blood stream, however, is that endorphins can totally suppress reproduction by suspending the release of GnRH from the hypothalamus (e.g., Figure 8.2). This, in turn, prevents sufficient synthesis and release of LH, and possibly FSH, from the gonadotroph cells in the anterior pituitary gland. Follicular development then stops at the antral stage for lack of enough oestradiol to trigger ovulation. As a result, plasma progesterone remains low since a corpus luteum is never formed from left-over follicular tissue (Abbott, 1987).

Besides totally suppressing reproduction in primates, social stress may also operate to only inhibit it (Abbot, 1987). For example, under normal conditions, as noted above, high concentrations of plasma progesterone are produced from the corpus luteum to enhance the success of embryo implantation and continued maintenance. But what happens to the level of progesterone if stress occurs at the exact moment of ejaculation, as with stumptail sexual interference? There is no direct evidence to support it, but what is proposed here is that interference during matings may produce enough stress on the mating female to cause the release of endorphins and

TABLE 8.1. Female primate reproduction suppressed by social stress: in this case by superior dominance rank (from Abbott, 1987).

Species	Population: Captive (C) Wild (W) Wild: Food Provided (WP)	Maximum Extent of Observed Reproductive Suppression	Study
Callithrix jacchus	C	Suppressed ovulation	Abbott, McNeilly et al. (1981)
Saguinus oedipus	C	"	French et al. (1984)
Saguinus fuscicollis	C	"	Epple and Katz (1984)
"	W	No offspring produced	Terborgh and Goldizen (1985)
Saguinus mystax	W	"	Garber et al. (1984)
Miopithecus talapoin	C	Supressed ovulation	Abbott et al. (1986); Keverne (1979)
Cercopithecus aethiops	W	Fewer offspring produced	Whitten (1983)
Macaca mulatta	C	"	Wilson et al. (1978)
"	WP	First successful conception delayed	Drickamer (1974); Meikle et al. (1984)
Macaca fuscata	WP	"	Sugiyama and Ohsawa (1982)
Macaca sinica	W	Fewer offspring produced	Dittus (1986)
Theropithecus gelada	W	Delay in successful conception	Dunbar (1980)
Papio anubis	C	Delay in onset of oestrus (and ovulation)	Rowell (1970)

FIGURE 8.2. Ovulation failure in female marmosets (Callithrix jacchus) produced by hormonal suppression and induced by social stress (e.g., subordinate dominance rank) (from Abbott, 1987).



these, in turn, either inhibit ovulation, inhibit conception, or lower progesterone level enough to discourage implantation. Males may also be effected by a reduction in viable sperm.

Stress-reduced reproduction is often doubted when applied to wild or free-ranging populations because it is commonly assumed that the level of social stress imposed on individuals in these circumstances is not sufficient to alter reproductive physiology (e.g., Deag, 1977). However, as pointed out by Rowell (1970) and Dunbar (1980), the levels of stress required to suppress reproduction may, in reality, be quite low; Rowell found that low dominance status, reinforced by occasional attacks, was sufficient to suppress reproduction in captive baboons, and Dunbar discovered that in wild baboons only 3.5 attacks per day, consisting mostly of simple threats and passive displacements, were enough to reduce by half the reproductive output of the 10th ranking female compared with the alpha female. Even though blood sampling and hormonal analysis will ultimately be necessary to conclude anything absolute about the effects of stress on fertility in free-ranging populations (Harcourt, 1987), the following results and reproductive data from this study, at least, suggest that stress-related variation in reproduction among individuals may be the purpose of sexual interference in stumptail macaques, ultimately benefiting those individuals who do the interfering.

RESULTS

To help examine the stress hypothesis, the following section will focus on mating data, especially the differences between matings with and without sexual interference. These differences will be presented generally, but also within and between individuals. Several specifics of matings

which receive interference will be looked at as well.

On Matings

When again considering the 5 categories of mating as presented in Figure 6.5, but this time distinguishing between matings with and without sexual interference, the category that becomes immediately obvious as different is mating duration (Figure 8.3). However, since this category is a sum of the two categories to ejaculation and tie, it can be seen that the only real difference between matings that received or did not receive interference was the length of the tie (Figure 8.3). Tie durations during matings with interference averaged 72.93 seconds, whereas tie lengths during matings void of interference averaged 46.62 seconds. This difference is highly significant (Mann-Whitney U test, $z = -2.75$, $p = .006$, 2-tailed). It is important to note that sexual interference and tie length are also positively correlated (Spearman rank correlation coefficient test, $r_s = .334$, $p < .001$).

Another interesting facet of the tie duration category becomes obvious when serial matings receiving interference are divided into two equal halves. Results show that tie durations average 67.10 seconds in matings in the first half of a series, while tie durations in the second half average 82.35 seconds (Figure 8.4). As with tie durations with and without interference, this difference is significant (Mann-Whitney U test, $z = -2.36$, $p = .018$, 2-tailed). Consequently, tie durations increase as a mating series with interference progresses.

If mean tie durations are presented by number of intruders, variations occur as well. Figure 8.5 graphs these differences according to how much they vary above and below the overall mean. As can be seen, the average tie for matings with 2 intruders was the shortest, while the average tie for

FIGURE 8.3. Mating behaviour with and without sexual interference. Durations are in seconds. T-bars represent top half of Standard Error. For further explanation see text and Figure 6.5.

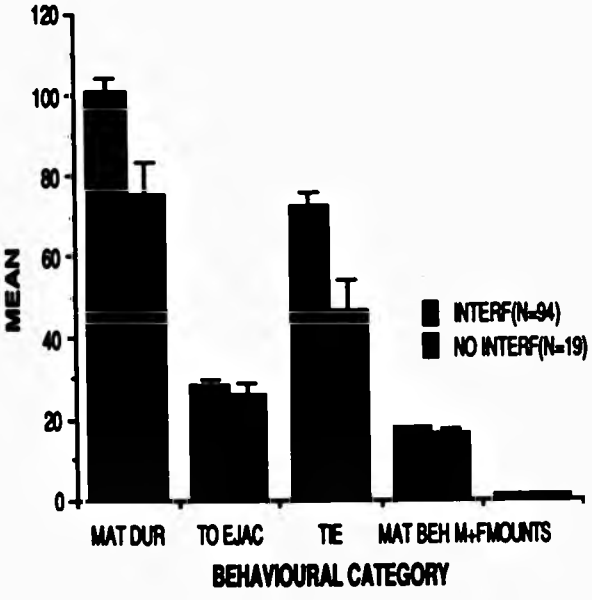


FIGURE 8.4. Mean tie durations of first and second halves of serial matings receiving sexual interference. T-bars represent top half of Standard Error.

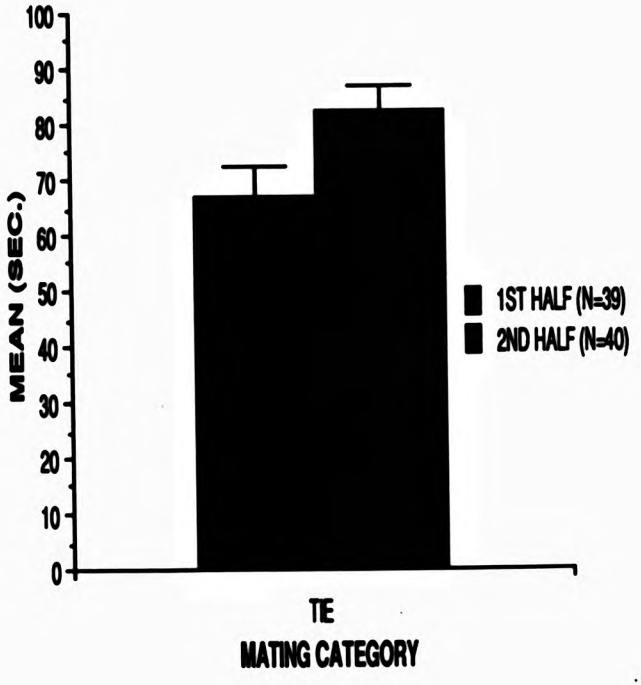
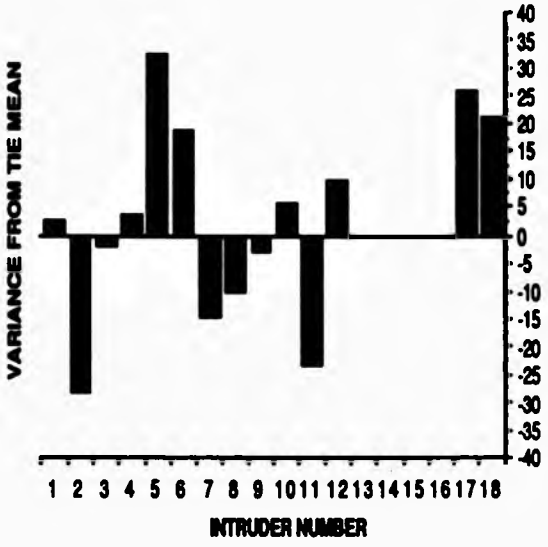


FIGURE 8.5. Variance from overall mean tie duration by number of intruders. Overall mean equals 72.93 seconds based on 86 eligible matings and is represented by zero. Variances are also in seconds and calculated by adding or substracting the difference of the mean score for each intruder category to or from the overall mean score. Matings receiving 13-16 intruders did not occur.



matings with 5 intruders was the longest. The other categories fall somewhere in between. Statistically, these differences are significant at the .05 confidence level (Kruskall-Wallis test, H(86)= 22.40, p= .049, 2-tailed).

Furthermore, even though the difference was not significant for the number of mounts each male required to reach ejaculation in matings with and without interference (Wilcoxon matched-pairs signed ranks test, z= -.730, p>.05, 2-tailed), it should be noted that the mean was 1.48 for the former circumstance and only 1.14 for the latter (Figure 8.6). In other words, males generally required more mounts to reach ejaculation in matings that were intruded upon.

On Individuals

As noted above, the area of mating that appears to be significantly altered by sexual interference is the duration of the mating pair's tie; overall, it increases. This effect of interference, however, is not distributed equally among all individuals who mate. Although the low frequency of matings without interference (17%) makes it difficult to compare, individuals of lesser dominance rank seem more effected. For example, among the two highest ranking males who participated in 92% (N= 104) of all the matings, McGregor, the beta male, showed a larger difference in his two types of tie lengths than did Pancho, the alpha male (Table 8.2). Grouped together, all male's of middle rank, like McGregor, showed a larger difference than Pancho (Table 8.2). And, even though McGregor's variation was not significant (Mann-Whitney U test, z= -1.53, p= .126, 2-tailed), his matings with interference were longer than without, while Pancho's and the other male's showed the reverse. This latter trend may be due to small sample sizes. For example, only two of Pancho's

FIGURE 8.6. Mean number of pre-ejaculatory mounts for matings with and without sexual interference. T-bars represent top half of Standard Error.

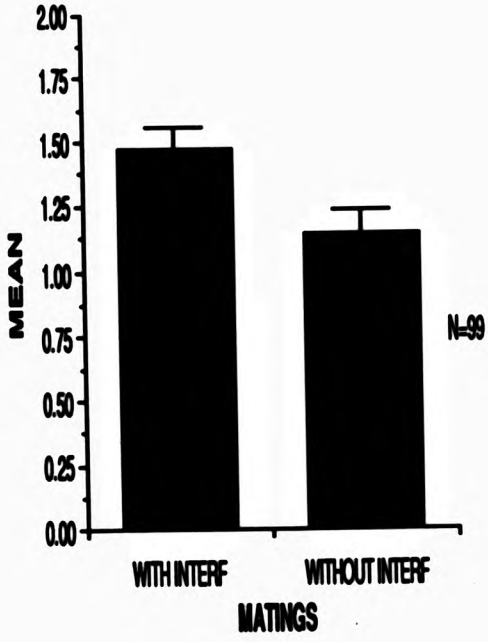


TABLE 8.2. Mean tie durations for males during matings with and without sexual interference.

	TIE DURATION					
	Matings					
	With Interference			Without Interference		
Male	Mean	N	SE	Mean	N	SE
McGregor	61.93	14	8.56	42.29	7	10.99
Pancho	75.69	71	8.58	78.50	2	9.50
Other	31.00	1	.00	38.25	4	11.24

matings were not interfered with, and only one mating of the other-male group was.

For the 4 females with matings with and without interference, rank order also seemed to affect tie length. Both Pierre and Flaca, ranked 5 and 6 respectively, showed less variation in their 2 forms of tie durations than did Bruja, ranked 15, and Rosy, ranked 21 (Table 8.3). This may have been partially dependent upon who these female's mated with most often (Figure 8.7). It appears that between Pierre and Flaca, the one who mated most with Pancho had the least variation. The same was true for Bruja and Rosy. Furthermore, Pierre and Flaca had longer tie lengths without interference than with, but just the opposite was true for Bruja and Rosy (Table 8.3). The difference in tie lengths for Bruja was significant (Mann-Whitney U test, $z = -2.62$, $p = .009$, 2-tailed). It was not, however, for Rosy (Mann-Whitney U test, $z = -.88$, $p > .05$, 2-tailed).

Tie lengths also vary during serial matings with sexual interference. Overall, when divided into matings occurring in the first and second half of a series, the latter half are significantly longer, as noted earlier. This is also true when such matings are looked at in terms of participants. Of the 8 individuals (2 males and 6 females) involved in serial matings, 6 had longer second-half tie durations. For the males, Pancho's first-half ties averaged 67.15 seconds. His second-half averaged 85.44 seconds (Table 8.4). This variation was significantly different (Mann-Whitney U test, $z = -2.60$, $p = .009$, 2-tailed). The variation for McGregor was not (see Table 8.4).

A similar circumstance existed for the females (Table 8.5). Pierre's, Flaca's, Lucia's, Bruja's, and Rosy's first-half tie durations, averaging 66.67, 70.00, 69.67, 65.33, and 56.50 seconds, respectively, were all shorter than their second-half durations, which averaged, in order, 83.60,

TABLE 8.3. Mean tie durations for females during matings with and without sexual interference.

	TIE DURATION					
	Matings					
	With Interference			Without Interference		
Female	Mean	N	SE	Mean	N	SE
Pierre	75.58	19	5.53	78.50	2	9.50
Flaca	85.80	10	16.49	98.00	1	.00
Bruja*	65.89	9	7.21	24.75	4	5.15
Rosy	62.50	18	5.06	49.50	2	12.50

* Significant difference (see text for statistic)

FIGURE 8.7 Pierre's(a), Flaca's(b), Bruja's(c), and Rosy's(d) mating distributions with males. Males presented in descending dominance rank order.

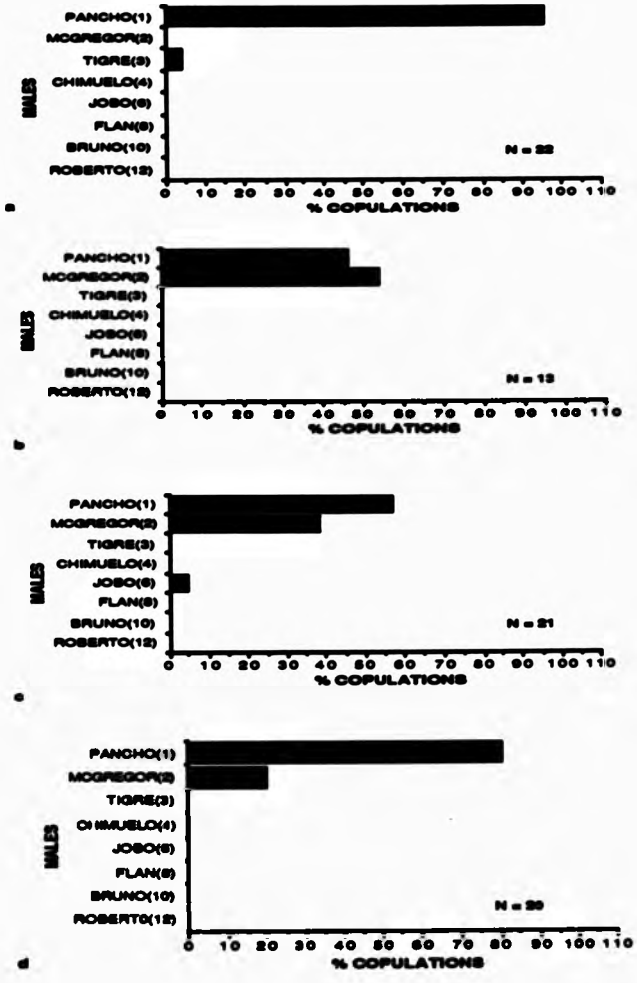


TABLE 8.4. Mean tie durations for males of first and second halves of serial matings receiving sexual interference.

	TIE DURATION					
	Serial Matings					
	1ST Half			2ND Half		
Male	Mean	N	SE	Mean	N	SE
Pancho*	67.15	33	5.55	85.44	34	4.55
McGregor	65.17	6	11.93	64.83	6	16.49

* Significant difference (see text for statistic)

TABLE 8.5. Mean tie durations for females of first and second halves of serial matings receiving sexual interference.

TIE DURATION

Serial Matings

	1ST Half			2ND Half		
Female	Mean	N	SE	Mean	N	SE
Pierre	66.67	9	9.72	83.60	10	5.08
Flaca	70.00	5	14.34	101.60	5	29.90
Fanny	87.75	4	31.62	64.25	4	6.70
Lucia*	69.68	9	10.17	93.33	9	5.18
Bruja	65.33	3	10.71	108.00	3	27.43
Rosy	56.50	8	6.99	74.50	8	6.67

* Significant difference (see text for statistic)

101.60, 93.33, 108.00, and 74.50 seconds. Also of these, the variation in Lucia's first and second halves was different enough to be significant (Mann-Whitney U test, z= -2.21, P= .027, 2-tailed). The other's variations were not. Only McGregor, of the males, and Fanny, of the females, showed longer first-half tie lengths (Tables 8.4 and 8.5). McGregor's first and second halves averaged 65.17 and 64.83 seconds, respectively, and Fanny's averaged 87.75 and 64.25 seconds. But again, neither of these variations differed significantly, and the general trend is for longer second-half tie durations within a series. To see whether longer second-half tie durations for serial matings might result from a change in the number of group members sexually interfering, figures for this were broken down for individuals as well (Figures 8.8 and 8.9). As can be seen, a trend exists toward fewer intruders interfering during the second half for 5 of 8 individuals, but this variation was slight and non-significant. In other words, the number of individuals interfering does not actually change from the first and second half in serial matings.

Between Individuals

Also interesting are differences between individuals when compared directly. Considering matings overall, variation in tie duration between males was considerable (Figures 8.10a and 8.11a). For example, Pancho's average tie length was 75.77 seconds, whereas for McGregor it averaged 55.38 seconds. For the remaining males grouped together, it was 36.80 seconds. The average tie overall was 69.48 seconds. When a Kruskall-Wallis test was run to measure the significance of this difference, it was found to be high (H(99)= 13.92, p= .001, 2-tailed).

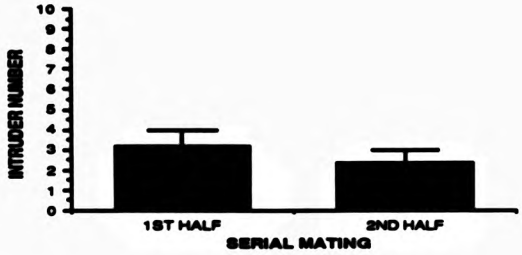
A similar circumstance was found for the females. Flaca had the longest average tie duration with 86.90 seconds, while the average tie for Elena,

FIGURE 8.8. Average number of intruders per serial mating by first and second halves for Pancho(a) and McGregor(b). T-bars represent top half of Standard Error.

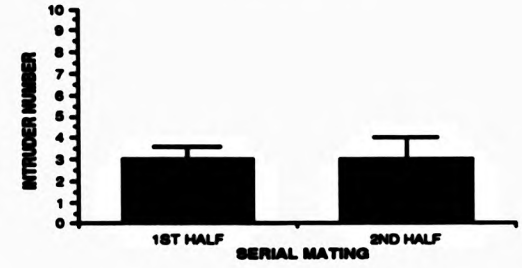
a

b

FIGURE 8.9. Average number of intruders per serial mating by first and second halves for Pierre(a), Flaca(b), Fanny(c), Lucia(d), Bruja(e), and Rosy(f). T-bars represent top half of Standard Error.



a



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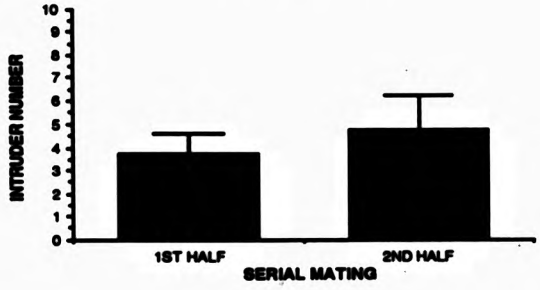
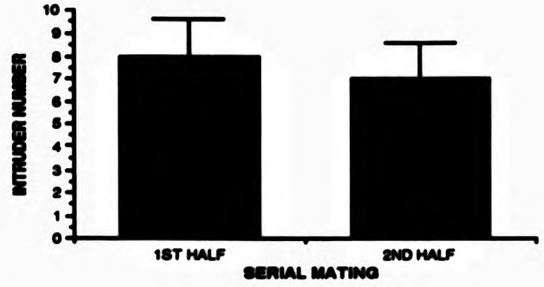


c

FIGURE 8.9. Continued.



d

e

f

FIGURE 8.10. Variation among males in tie duration: (a)overall, (b)with, and (c)without sexual interference. Durations are in seconds and T-bars represent top half of Standard Error.

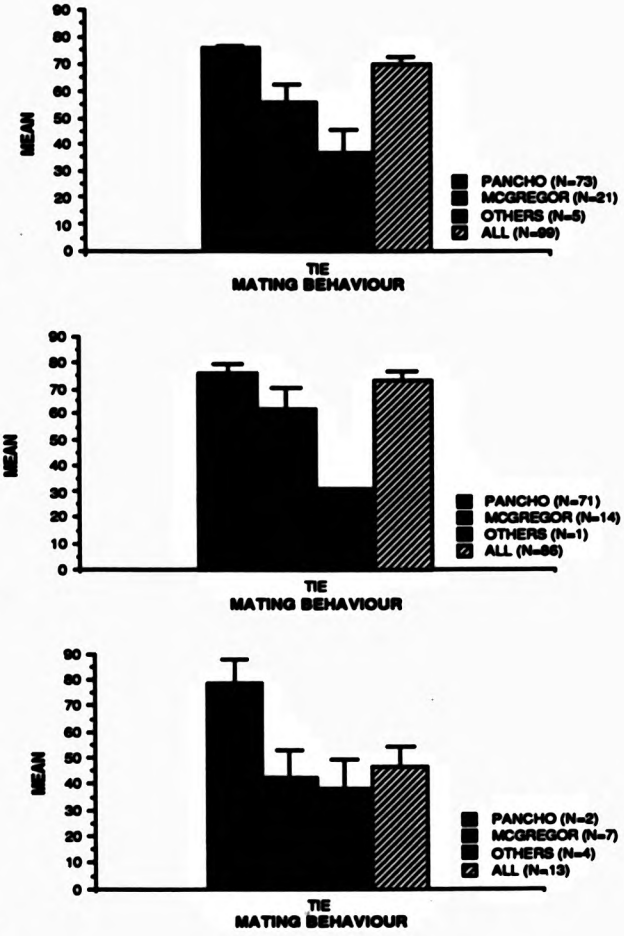
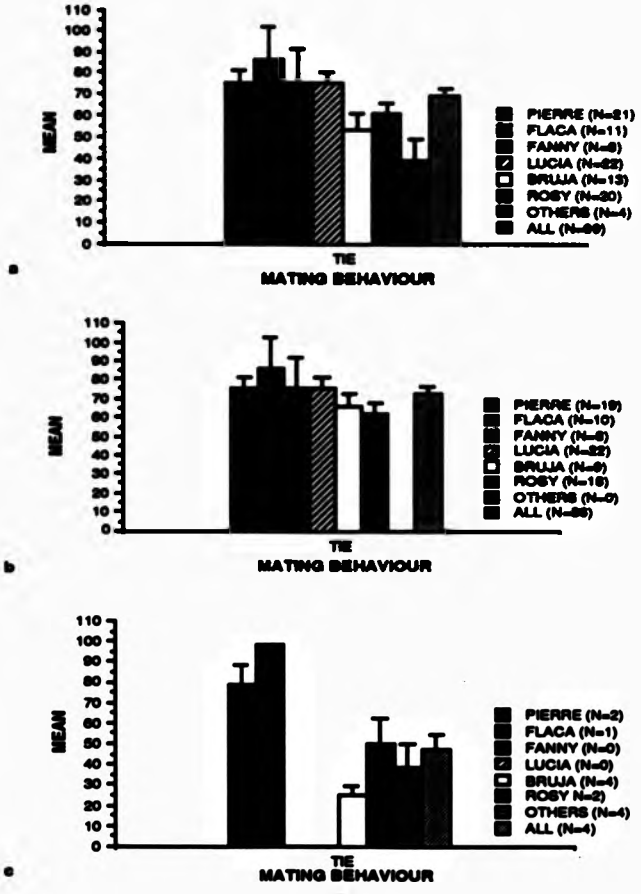


FIGURE 8.11. Variation among females in tie duration: (a)overall, (b)with, and (c)without sexual interference. Blank column(s) represent all matings had interference (c), or the reverse (b). Durations are in seconds and T-bars represent top half of Standard Error.



Ucilia, Flossie and Canela grouped together was 38.25 seconds. With Pierre, Fanny, Lucia, Bruja, and Rosy recording various averages in between, the difference between females, like males, was highly significant (Kruskall-Wallis test, H(99)= 15.63, p= .016, 2-tailed). It is interesting to note a trend in males and females: increased rank seems to equal increased tie duration, hence a better theoretical chance at insemination, but more interference, at least for males.

When these overall tie durations for the males and females were broken down into both those with and those without sexual interference (Figures 8.10b-c and 8.11b-c), the differences still varied considerably, and significantly for males with interference (Kruskall-Wallis test, H(86)= 6.23, p= .044, 2-tailed). The variations among individuals for the other 3 categories did not reach the .05 significance level.

Concerning sexual interference, the number of individuals interfering with matings greatly depended upon who was involved. Among the males, the alpha male, Pancho, received the largest number with an average of 4.77 per mating (Figure 8.12). McGregor experienced 1.94 per mating, while Tigre and Jobo received 3 each, but both of these were based on a single mating apiece. For females, Lucia received the most with 6.91 per mating, and Canela the least with 1 intruder per mating (Figure 8.13). Canela's score, however, like Tigre and Jobo among the males, was a result of only a single mating. The difference among females was significant (Kruskall-Wallis test, H(88)= 23.06, p= .001), whereas for males it was not (Kruskall-Wallis test, H(94)= 6.44, p= .092).

And finally, when considering the interval between ejaculations, Pancho's average of 17.82 minutes was less than McGregor's of 23.38, but not significantly (Mann-Whitney U test, z= -.660, p>.05). Among the females, intervals varied from a low of 8.29 for Fanny to a high of 26.30

FIGURE 8.12. Average number of intruders per mating for males. Blank columns represent matings without interference. Listed by dominance rank order. T-bars represent top half of Standard Error.

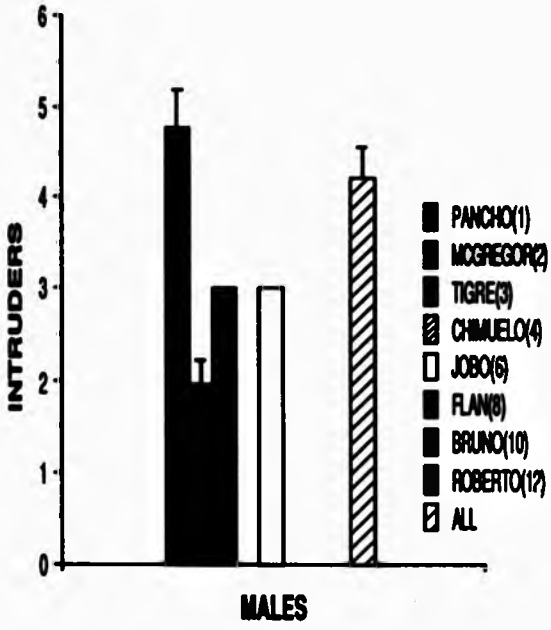
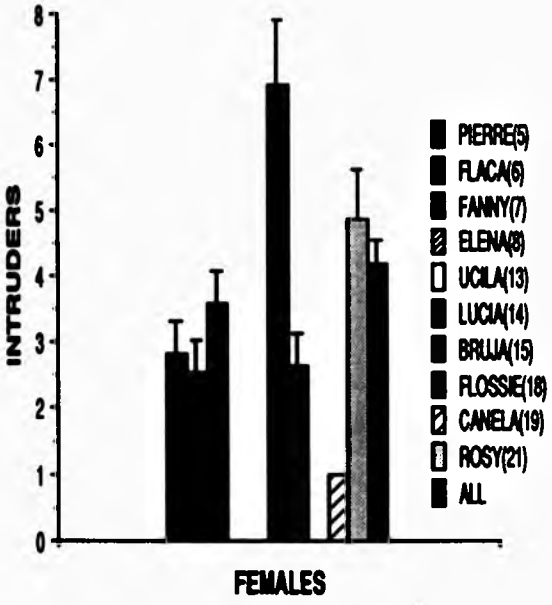


FIGURE 8.13. Average number of intruders per mating for females. Blank columns represent matings without interference. Listed by dominance rank order. T-bars represent top half of Standard Error.



minutes for Flaca, which was a highly significant difference (Kruskal-Wallis test, H(77)= 21.40, p= .001) (Figure 8.14 and 8.15, respectively).

REPRODUCTIVE DATA

Historical

The group's reproductive history is summarized in Table 8.6. It is presented by both individual female and matriline. Figures for the group as a whole are also provided. Paternity, however, is unknown.

By reviewing the table, even though there are no significant differences between individuals or matrilines in age at first giving birth, number of live births, and mean interbirth interval, it is obvious that considerable variation still exists, particularly among individuals. For example, with age at first giving birth, the group's overall mean was 60.10 months. At the same time, however, individual range varied from 42 to 90 months (Figure 8.16).

Considerable variation also exists between individuals with number of live births. Five matriarch females, who represent 5 of the group's 7 matrilines, provide lifetime reproductive data (see Prediction 7, this chapter). The range varies from 4 births for Jarocha to 9 births for Flor (Figure 8.17), averaging 6.6 births per female. And for at least these 5 females, the number of offspring produced by each was inversely correlated with the dominance rank of their matriline (Spearman rank correlation coefficient test, r_s= -.975, p= .002).

Concerning intervals between births, the average for the group was 21.30 months, but, again, the variation between individual females was

FIGURE 8.14. Average interval between matings for males. Listed by dominance rank order. T-bars represent top half of Standard Error.

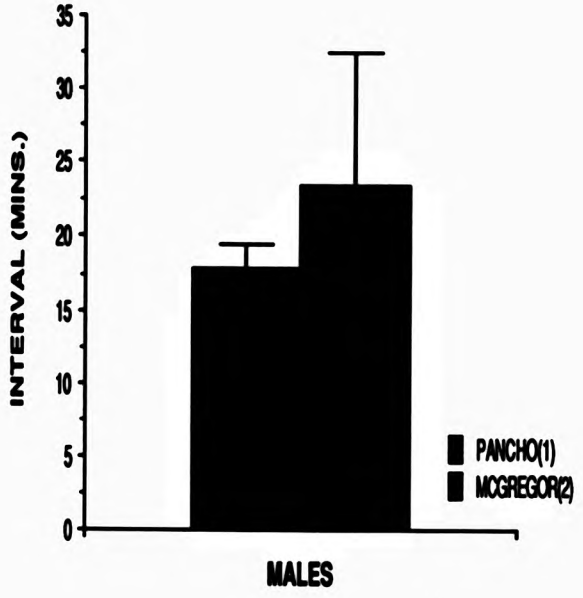


FIGURE 8.15. Average interval between matings for females. Listed by dominance rank order. T-bars represent top half of Standard Error.

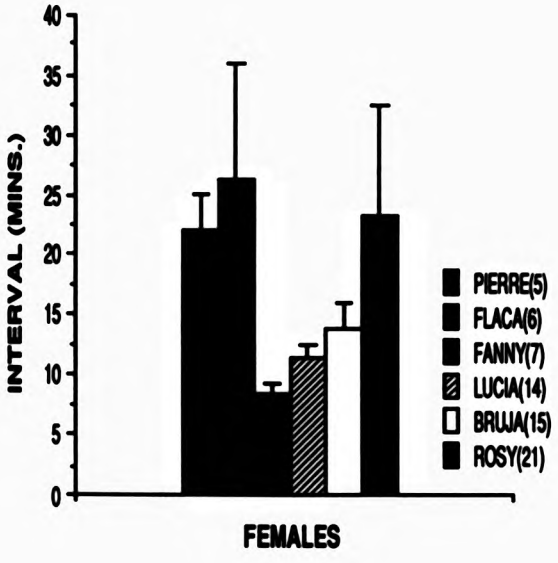


TABLE 8.6. Summary reproductive data of the Tanaxpillio stumptails over a period of 15 years from April, 1972 to March, 1987 while they were in both Puerto Rico and Mexico. Presented by female and matriline according to descending matrilineal dominance rank.*

Female/ Matriline	Age at First Giving Birth (Months)	Number of Live Births (N)	Sex Ratio (M:F)	Mean Interbirth Interval (Months)	Range (Months)
Jarocha	?	4	3:1	22.33	15-35
Mean:	?	4.00	3.0:1.0	22.33	15.0-35.0
Margarita	?	6	2:4	15.00	08-20
Pierre	57	4	1:3	31.00	17-58
Enriqueta	-	-	-	-	-
Piedad	60	1	0:1	-	-
Mirna	42	3	2:1	23.50	21-26
Martha	52	1	1:0	-	-
Marcela	57	1	1:0	-	-
Mean:	53.60	2.67	1.4:2.3	23.17	15.3-34.7
Fiaca	?	7	2:5	19.50	08-25
Negra	-	-	-	-	-
Elena	73	4	2:2	23.00	18-30
Ucilia	49	2	2:0	21.00	21
Fanny	90	1	0:1	-	-
Flavia	55	1	0:1	-	-
Mean:	66.75	3.00	2.0:2.3	21.17	15.7-25.3
Blondie	?	7	3:4	21.17	16-25
Bruja	57	4	3:1	20.00	17-23
Lucia	57	3	0:3	21.00	17-25
Biasita	57	1	0:1	-	-
Mean:	57.00	3.75	3.0:2.3	20.72	16.7-24.3
Flor	?	9	5:4	14.25	10-19
Rosy	55	4	1:3	27.00	17-44
Sigri	69	1	1:0	-	-
Lolita	50	4	2:2	22.33	19-25
Canela	71	2	0:2	23.00	23
Flossie	67	1	0:1	-	-
Mean:	62.40	3.50	2.3:3.4	21.64	17.3-27.8
Blanca	52	4	2:2	21.00	18-23
Teresa	63	2	1:1	20.00	20
Mean:	57.50	3.00	1.5:1.5	20.50	19.0-21.5
Bonita	59	2	0:2	17.00	17
Juanita	70	1	0:1	-	-
Mean:	64.50	1.50	0.0:1.5	17.00	17.0-17.0
MEAN:	60.10	3.08	2.0:2.1	21.30	16.6-27.0
SE:	2.29	.44	.26:.27	.97	1.04-2.49
RANGE:	42-90	1-9	1-5:1-5	14.3-31.0	8-23/17-56

* Based on births only. Records supplied by Cabe-Vinagre (pers. comm.).
? Unknown

FIGURE 8.16. **Female age at first giving birth for the Tanaxpillo stumptails over a 15 year period. Each grouping represents a seperate matriline. They are presented in descending rank order.**

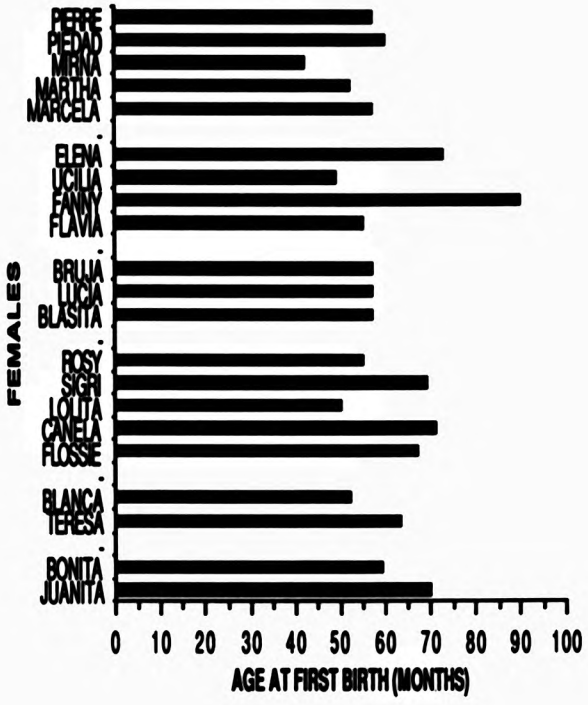
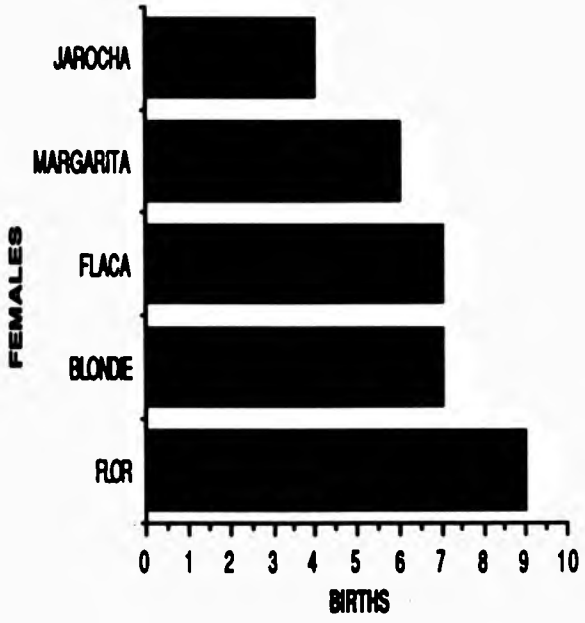


FIGURE 8.17. Number of live births among the females Jarocha, Margarita, Flaca, Blondie, and Flor. Each number represents a life-time of reproduction. The females are from seperate matrilines and are presented in descending rank order.



great (Figure 8.18). At the lower end of the range, the mean interval for Flor was only 14.25 months, while for Pierre, at the opposite extreme, it was as long as 31 months.

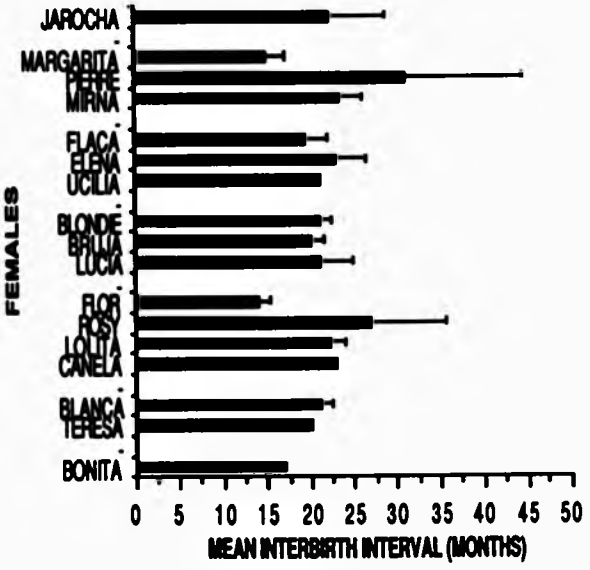
Study Period

According to updated information, from the 113 matings recorded during the field phase of the present study, only 1 infant was conceived: a male named Brujo born to Bruja on 12 July 1984. If an average gestation length of 177 ± 2.1 days is used to count backwards to help determine the possible matings leading to conception (MacDonald, 1971), all matings witnessed during this particular oestrous cycle include the following (listed by date, time, mating male, and number of intruders):

(1) 13 January, 15:03, McGregor, 2
(2) 13 January, 15:15, McGregor, 1
(3) 17 January, 11:32, Pancho, 4
(4) 17 January, 11:49, Pancho, 1
(5) 20 January, 10:13, Pancho, 7
(6) 20 January, 10:22, Pancho, 5

Again, using the 177± 2.1 day average for gestation, peak receptivity probably occurred between 15 and 19 January, with 17 January being the most likely day of ovulation. Interestingly, both matings on the peak day were with Pancho, the alpha male. I suggest then that the mating responsible for Brujo's conception may have been the one at 11:49 on 17 January. This is because the mating at 11:49, if interference does stress the mating pair, had a lower combined score (CS=143) than the mating at 11:32 on the same day (CS=1437). The tie length and amount of

FIGURE 8.18. Mean interbirth intervals for the Tanaxpillo females over a 15 year period. Each grouping represents a separate matriline and they are presented in descending rank order. T-bars represent top half of Standard Error.



interference during the probable conception mating, compared with the mean for each, are presented in Figures 8.19 and 8.20. However, it should be noted that the mating which led to insemination may not have been observed, although between 10-20 January only one day of observation was missed: the 15th.

THE SPITE HYPOTHESIS

As noted in Chapter 5, a spiteful act is one that runs the risk of reducing the reproductive fitness of both the recipient and perpetrator of the action, and is, according to Hamilton (1971), behaviour better classified as "strongly" spiteful. By analogue, this is represented by a double negative (-,-) which signifies a net cost in fitness for both individuals. But since every action costs something, what is of actual importance to the actor is the relative outcome in overall costs and benefits between himself or herself and the recipient (Hamilton, 1970). An action may be equally costly to both parties (strongly spiteful), but can continue to be classified as spiteful as long as the actor ends up without benefiting directly (Hamilton, 1971). This is represented by analogue by a zero and a negative (0,-). Therefore, it is not necessary that a loss in reproductive fitness be demonstrated, only that the risk of a loss exists, even though this is admittedly difficult to measure in precise quantitative terms (Pierotte, 1982). For example, how does one measure the risk of an act which may result in death or serious injury for an actor when the actor escapes unharmed? It is essentially unmeasurable, but this does not make such a risk any less real or a spiteful act any less spiteful (Pierotte, 1982). It is proposed than that since those who intrude run the risk of being physically harmed by the mating male (e.g., 3% of the matings involved retaliation), even if they are not, while

FIGURE 8.19. Tie duration of possible conception mating compared with mean tie duration for matings overall. T-bar represents top half of Standard Error.

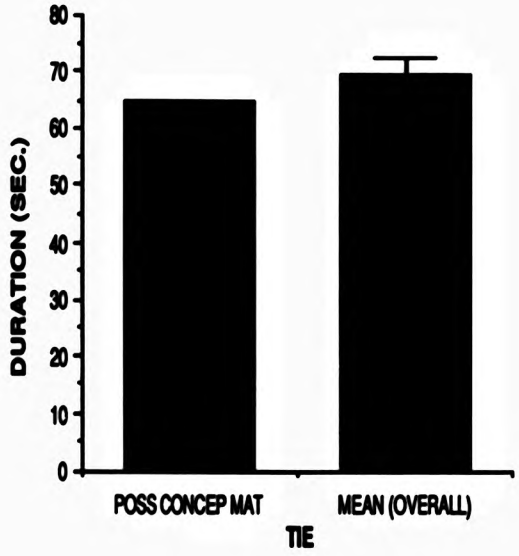
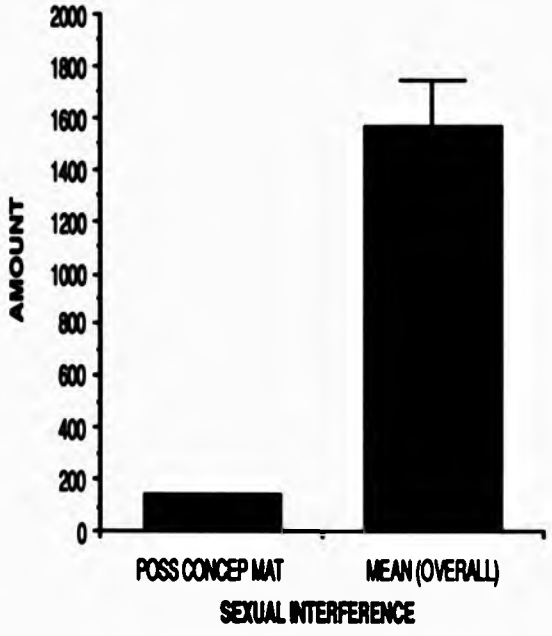


FIGURE 8.20. Amount of sexual interference determined by total intruder combined score for possible conception mating compared with the mean combined score for mating overall. T-bar represents top half of Standard Error.



at the same time they potentially reduce his and the mating female's reproductive fitness, sexual interference in stumptail macaques qualifies as spiteful behaviour. What makes this more likely is there appears to be no immediate resource for which the intruders are competing. In other words, an intruder was never observed in this study to attempt to mate with the opposite sexed member of the pair upon whose mating they had intruded, and without a resource, the probability of the behaviour being selfish is reduced. Other examples of spiteful behaviour in primates are harassment of one female by another in gelada baboons (Dunbar, 1980) and, in macaques, kidnapping attempts by unrelated females of each other's infants (Silk, 1983).

But, even if interference in stumptails is spiteful, by what method can it reduce the fitness of mating individuals? As proposed earlier in the chapter, it just may be through social stress. Stress can prevent conception in some primate species altogether, as already shown, and can also lengthen the interval between births. These two circumstances in themselves can have substantial reproductive consequences for both males and females over a lifetime.

As reasonable as this hypothesis is, however, does the circumstantial data of the present study minimally support it? The answer offered here is tentively yes, and the remainder of the chapter will be concerned with presenting tests of evidence.

Predictive Tests

Accordingly, the predictive tests concerning the likely effect of sexual interference on matings in stumptails, if stressful, are the following:

(1) *Results:* Tie durations of matings with interference should differ from those without, if tying increases the probability of conception.

(2) *Results:* Tie durations of matings at the end of a series should differ from those at the beginning.

(3) *Results:* The number of mounts it takes a male to reach ejaculation should increase with matings with interference opposed to matings without.

(4) *Results:* Duration between ejaculations should vary among individuals.

(5) *Reproductive Data:* Age at first giving birth should vary among females,

(6) *Reproductive Data:* as should intervals between births,

(7) *Reproductive Data:* and number of live births produced over a lifetime.

Each of these tests will now be addressed in turn.

DISCUSSION

Evidence

Results

Predictive Test 1. The first set of indirect evidence suggesting that sexual interference effects mating is differences in tie durations between those that receive interference and those matings that do not (Figure 8.3). On average, ties of matings with interference are 56% longer than ties of matings without, and this difference is significant. Also, there is a direct and positive correlation between sexual interference and the length of the tie. In other words, among matings with interference, the greater its amount, the longer the ties. But why should this be, and why is it that some individuals' tie lengths are effected, while others are not? Among the males, McGregor's (Figure 8.21) ties were greatly effected, but Pancho's (Figure 8.22) ties were not (Table 8.2); among the females, Bruja's and Rosy's durations were highly effected, Bruja's significantly, whereas Pierre's and Flaca's tie lengths changed very little with interference.

If intrasexual competition is the primary motivation behind sexual interference (as proposed earlier in this chapter), and the purpose of tying is to increase the likelihood of conception (as proposed in Chapter 6), one would reasonably suspect that the purpose of interference is to decrease the length of ties in order to make the possibility of conceptions less likely. But the exact opposite seems to occur. Tie lengths increase with interference, rather than decrease. So why do group members even bother to interfere? I suggest they do because interference does decrease the likelihood of conception and longer tie-lengths may actually demonstrate this, even though it is the reverse of what one might expect. There is no direct evidence for it, but there just may be an optimal period where a tie is

FIGURE 8.21. The beta male, McGregor.

FIGURE 8.22. The alpha male, Pancho.

more likely to lead to conception, and anything longer or shorter makes this possibility more remote. Future research in the laboratory could clarify this point, as it could also test whether pairs of stumptails housed separately are more fertile than those housed in a group. But both are yet to be done. It is also recognised that with tie duration an optimal argument is more difficult to support than an argument of linearity; intra-individual variation (see Tables 8.2 and 8.3) may present a problem as well. Again, more data is needed to help clarify these points.

Even so, I tentively propose that the overall excitement of sexual interference stresses the mating pair enough for the male to end up responding by extending his tie lengths by an average of 56% over ties where interference is absent. The fact that tie durations of alternative matings void of interference are significantly shorter than ties of normal matings with interference (see Chapter 9) makes this suggestion more likely. However, since the tie lengths of individuals are not effected equally, those of higher dominance rank (Pancho, Pierre, and Flaca) may be effected less overall than those of lower dominance rank. So high rank may be important to acquire if for no other reason than to help suppress the immediate effects of sexual interference.

Predictive Test 2. If true, and sexual interference does place stress on individuals while mating, what other supporting evidence does this study offer? Significantly longer tie durations overall in matings occurring in the second half of a series may be relevant (Figure 8.4). By individuals, 6 of 8 had longer second half ties (Tables 8.4 and 8.5), and for 2 of these, Pancho and Lucia, the variations were significant. This again might suggest that interference is stressing the mating pair since tie lengths increased on average 23%. Even high ranking individuals are not exempt, and particularly not Pancho; his second half ties increased 27%. However,

could this phenomenon be accounted for by male fatigue? In other words, as a series progresses, does the male tire and, therefore, remain tied longer? This is possible, but unlikely, since Estep et al. (1984) found that tie durations are longest during the middle phase of a series, rather than the late phase.

Predictive Test 3. What other circumstantial evidence is there for this hypothesis? Even though the difference was not significant, but a trend, the fact that the average number of mounts required by a male to reach ejaculation was greater during matings with interference (1.48) than without (1.14) might suggest again that mating pairs are being stressed (Figure 8.6). When potential intruders move toward a pair in anticipation of a mating about to occur, as they most always do, it is possible that some degree of stress is being imposed, and in this case, enough to increase the number of required mounts for ejaculation by 30%.

Predictive Test 4. One final bit of evidence from the results section of this study that may also suggest that interference places stress on mating individuals is the amount of time it takes between matings. If individuals are stressed, then it would seem reasonable that certain individuals would be effected more than others depending upon how much sexual interference each receives. Generally, what should be expected is the greater the amount of interference, the longer the interval between matings. The dominance rank of the males and females involved may reduce the interval somewhat, but certainly dominance alone cannot explain the large degree of variation recorded among individuals found in this study (Figure 8.14 and 8.15). But rank, in combination with stress caused from sexual interference just may. Because the study offers so few matings in a series void of interference, this suggestion is preliminary and awaits further data and analysis.

Reproductive Data

After running relevant statistical tests on the group's reproductive data as listed in Table 8.6, it was found that females and matrilines do not vary enough among themselves to be considered significantly different within the three important categories of age at first giving birth, number of live births, and mean interbirth interval. In theory, however, this is not surprising. Excluding independent external variables, different females of the same species living in an identical environment should vary only slightly among themselves in the three categories. These slight differences can probably be explained by the unique physiology of each female concerned. But when the differences among females are more than slight, some external influence may well be involved. The present data, even though not significantly different, may reflect this. It should also be remembered that even if reproductive variations among females are small, and even if not statistically significant, the mechanism(s) responsible (e.g., behaviour) may still contribute to long-term fitness (Silk, 1987).

Predictive Test 5. When considering the age that females first give birth, it can be quickly seen from Figure 8.16 that definite and considerable differences among individuals do exist. Over the group's 15-year history, the earliest age that any female produced an offspring was 42 months. The oldest primiparous female was 90 months. So, if the matings of the female who took the longest to first reproduce had consistently received a greater amount of interference then the matings of the female who reproduced at the youngest age, it is conceivable that interference may have been stressful enough to delay initial conception in the former female. Long-term data on interference and other possible determining factors will, of course, be required to clarify this.

Predictive Test 6. Stress may also be responsible for the relatively large

variation among females in their mean intervals between births (Figure 8.18). A low of 14.25 months for Flor, as opposed to a high of 32 months for Pierre, can be seen. This test awaits long-term data as well, but the influence of stress on mating females may be more suggestive when looking at actual births.

Predictive Test 7. The 5 females presented in Figure 8.17 were all born in the wild and headed matrilines. Margarita and Flor had both died prior to the study, and the 3 others (Jarocha, Flaca, and Blondie) had stopped reproducing, most likely from old age. So the number of offspring each produced represents lifetime reproduction. As can be clearly seen from Figure 8.17, a substantial variation exists between the female who gave birth to the least number of offspring and the female who gave birth to the most: Jarocha produced 4 offspring, while Flor produced a total of 9. Six infants were born to Margarita and 7 apiece to both Flaca and Blondie. Again, this is a considerable variation, even if not a statistically significant one. What is significant, however, is the inverse correlation between the number of offspring that these females gave birth to and their descending order of dominance by matriline. In other words, the lesser their dominance, the greater their number of offspring. But why should this be? I suggest again that the amount of sexual interference a female receives over a lifetime of matings may be at the very least partially responsible. Knowing that the average number of intruders per mating among the group's females varied significantly, as demonstrated in Figure 8.13, adds support to this possibility. Also, from Figure 8.11, it can be seen that tie length tends to decrease with lower female social rank. In other words, if longer tie lengths bring greater interference to higher ranking females, hence, more stress, reproductive success may be reduced. In addition, a recent finding by Nieuwenhuijsen et al. (1985:92) found that, unlike rhesus

and Japanese macaques, most female stumptails experience "...several nonconceptive ovulatory cycles..." before conceiving. Their finding is based on a study of a group of 92 stumptails kept in a large outdoor enclosure. They offer no explanation, but speculate that a luteinized unruptured follicle syndrome (ovulation failure) (Koninckx et al., 1980) may be responsible. If true, I suggest that stress from sexual interference may be its cause, but, of course, this will take further, in depth, research to verify.

COMPARISONS OR FURTHER TESTS

With this now said, how do the relevant data of others compare as further tests?

Stumptails

If lengthened ties are evidence that sexual interference does effect mating, what comparable data is there? Of the 3 stumptail interference studies of Gouzoules (1974), Niemeyer (1980; Niemeyer and Chamove, 1983), and Bruce (1984) (see latter half of Chapter 2 for more detail), only Niemeyer and Bruce presented information about tie lengths during matings with and without sexual interference. Niemeyer found that there was only a slight difference between the two. Tie durations without interference had a mean of 70 seconds, while those with interference averaged 71 seconds. However, her results may not be truly reflective because of the confined nature of the group she was studying (personal observation). In other words, since her subjects were really never out of sight of each other, tie durations of matings without interference may have been abnormally long.

In support of this, Bruce found something different. Even though her

study was still conducted under captive conditions, her subjects had an almost 8 times greater living space than Niemeyer's subjects (432.78 m^3 opposed to 54.28 m^3), and this may reflect the difference in her findings. She found that tie durations were significantly longer during mating when interference was present than when it was absent, or, to be more accurate, 81 seconds with interference compared with 43.2 seconds without [$t(72)=4.19$, $p<.01$]. She had also predicted this outcome based on the literature. So, at a minimum, Bruce's study supports the finding of this study that stumptails under more "normal" conditions show longer tie lengths in response to sexual interference. Again, this may reflect that stress is being imposed causing the male to respond by tying longer.

Furthermore, even though other studies did not present data for number of mounts or durations between matings in a series, a study of Bruce's group by Estep et al. (1984) discovered that tie durations occurring during the two later phases of serial matings were significantly longer than those of the earliest phase. For matings pooled into phases of early, middle, and late, tie durations for the earliest phase averaged 66.6 seconds, whereas the latter two phases combined produced a mean of 100.2 seconds (One-way analysis of variance, $f=15.48$, $p<.08$). This is similar to what this study found and may reinforce the possibility that males are lengthening their ties in response to the imposed stress that interference may be producing. Again, further research is needed before this can be accurately verified.

Other Macaques

But what about the reproduction in other species of macaques where the phenomenon of sexual interference occurs much less? In other words, for example, are stumptail macaques slow or fast breeders compared with other species, thereby giving or not giving support to the idea that interference

may be responsible?

As noted above, female stumptails normally take several ovulatory cycles to conceive while rhesus and Japanese macaques commonly take one. Female stumptails are also known to take longer to first give birth and to reproduce thereafter (Nieuwenhuijsen et al., 1985; see also *Macaca* Review section in Chapter 6, and Table 6.1). The age at first birth in stumptails is between 53 and 60 months, while most other macaques take less (e.g., 43.3 months for rhesus). Only the Crested macaque is known to take slightly longer (66 months), and Japanese and Toque macaques appear to be about equivalent (60 months). Female stumptails also seem to take the longest amount of time between births (from 19.1 to 21.3 months). Rhesus take as little as 12 months. Stumptails appear then to be slow breeders in comparison with most other macaques. These behavioural and physiological differences may exist in stumptail macaques because interference places sufficient stress on mating pairs to suppress fertility [see Wasser and Barash (1982) for a review of stress related reproductive suppression in female mammals]. Again, this proposal is preliminary and further research is necessary for clearer demonstration of the affect of stress on mating behaviour. But, even if sexual interference is found to be stressful, and this is labelled spiteful, how does spite result in a return-benefit, as suggested earlier? This is the subject of Chapter 9.

CHAPTER 9

SEXUAL INTERFERENCE: AS RETURN-BENEFIT SPITE?

As proposed in the last chapter, the act of sexual interference may be classified as spiteful behaviour. But, as also pointed out, spitefulness in itself never ends in a net gain in reproductive fitness for those who choose to be spiteful. So, again, why would one choose to interfere? This is the subject of the present chapter. Briefly, the constraint-free reproductive strategy and alternative tactics of social primates, including stumptails, will be addressed. Some final results and explanations will also be presented.

CONSTRAINT-FREE REPRODUCTIVE STRATEGY

For individuals living in groups, competition for any resource that is limited, including mating partners, is common. Also common are specific strategies used by individuals to meet this competition. A strategy is defined as behaviour employed to obtain a specific end, usually reproductive fitness, without any foreknowledge implied (Hrdy and Williams, 1983). When one strategy is pursued over all others, it is referred to as *constraint-free*. It is considered this because of its high yield, and it is the strategy that individuals would ideally choose if there were no

competitive constraints over their choice of pursuit (Dunbar, 1982, 1988).

According to Dunbar (1988), the constraint-free reproductive strategy of group living primates competing for mates is dominance. In other words, the intrinsic power of high rank confers priority of access to mates. This is particularly true for males since they compete directly for the opportunity to inseminate females. However, for females, the importance of high rank is generally not as immediate. They are more likely to gain reproductively by having greater access to food and social partners, which benefits both them and their offspring in the long term (Hrdy, 1977; Dunbar, 1988). But since females may directly compete for quality sperm from high-ranking males (Small, 1987), high rank may serve as a constraint-free reproductive strategy for them as well.

ALTERNATIVE REPRODUCTIVE TACTICS

Not all primate group members, however, are equally capable of attaining high dominance rank. Are these individuals then prevented from reproducing throughout their lifetime? For females, this is unlikely since through their own manouverings there should always be at least some acceptable males available and willing to mate with them, males who out-rank other competitive females who may otherwise prevent the mating. On the other hand, low-ranking males have the potential of being severely reproductively suppressed. However, there are ways that lower-ranking individuals, both males and females, can go about improving their own rate of reproduction, and these are by employing alternative tactics (Dunbar, 1982, 1988). Tactics can best be described as less than ideal methods of achieving a specific goal, such as reproductive fitness. They are less than ideal because seldom are they as successful as using a primary strategy,

such as high rank. But if high rank, for example, can not be obtained, alternative tactics provide lower-ranking individuals with at least the opportunity to make marginal reproductive gains. Each individual should attempt to maximise reproduction in the best manner possible since evolution occurs at this level and not at the group's.

Stumptail Tactics

So what reproductive alternatives are there for stumptails who are of lower dominance rank? From the findings of the this study, alternative reproductive tactics for stumptails are of two types, those employed mainly by females and those practised primarily by males. These categories are not mutually exclusive, but they do represent what was generally observed in the field. Both sexes must cooperate with each other for either tactic to be successful. Having said this, one tactic consistently used by both sexes was sexual interference. The possible effects of this behaviour on one's competitors were described in the previous chapter. Interference may not contribute to one's fitness directly, but when used in combination with those tactics that could, relative gains can be made. The tactics that may contribute directly, and may possibly be implemented to avoid interference, are as follows: "female leave", where an oestrous female moves silently off from the main body of the group followed by a male suitor prior to mating [similar to what females have been observed to do in rhesus macaques (Brereton, 1981)], and "male hide-and-hurry", where a male avoids the attention of the other group members while rapidly mating with a cooperative female [often seen in other primates, e.g., rhesus macaques (Ruiz de Elvira and Herndon, 1986)]. The female leave tactic is not strictly limited to lower-ranking females, whereas the male hide-and-hurry tactic is more often restricted to lower-ranking males. What generally happens is

this:

> *For the female leave tactic, an oestrus female, after the group has been provisioned, for example, quickly glances at a male suitor (usually the alpha or beta), and then starts walking rapidly and silently off to an area 25 meters or more away. The area is often visually removed from the other group members as a whole, and they usually pay little attention, or do not notice at all, and continue feeding. While she does this, the female also glances back to see if the male she solicited is following, which he most often is. They then mate, with little or no sexual interference, and then return to feeding themselves.*
>
> *The male hide-and-hurry tactic is different. Here, a male mates with a cooperative female who is already on the group's periphery. An example of this is when the group changes from one of the islands of Tanaxpillo to the other. After most of the group members have transferred, a few individuals of both sexes lag behind. And when others are ahead and out of sight, a male often quickly mates with a willing female, again, with very little or no interference.*

The results of both these tactics are presented below.

RESULTS

The following general results will first present the frequency with which alternative tactic matings were recorded in this study, and then compare the amount of sexual interference they received on average with the other

matings. Tie durations for both categories will also be compared. Interference and tie durations will then be specifically compared for the two types of alternative tactic matings both overall and between individuals.

General

Firstly, the rate of alternative tactic matings recorded in the present study was 26.5% (N=30). This compares with 73.5% (N=83) for matings that did not involve alternative tactics (Figure 9.1). Of the former, 66.3% (N=19) were classified as female leave matings, while 36.6% (N=11) qualified as male hide-and-hurry.

Furthermore, of the 19 matings recorded in the study which lacked interference, 16 of them were alternative tactic. In other words, 84.2% (N=16) were of the alternative type, while 15.8% (N=3) were not (Figure 9.2).

When these two categories of matings are first broken down separately into those that received interference and those that did not, alternative tactic matings received interference far less often than did normal matings. The proportions of alternative matings with and without interference were 46.7% (N=14) and 53.3% (N=16) respectively, compared with 96.4% (N=80) and 3.6% (N=3) respectively for the other matings (Figure 9.3).

With respect to the actual intensity of sexual interference received by both categories of matings, the alternative category again experienced considerably less than did the other. An alternative mating had a mean combined score of 259.5, whereas a normal mating had an average of 2043.6. The overall mean was 1572.7 (Figure 9.4a). A Mann-Whitney U test revealed a highly significant difference between the two categories ($z = -6.30$, $p < .01$, 2-tailed).

When tie durations are compared for alternative and normal matings, a

FIGURE 9.1. Percentage of alternative tactic matings observed out of the total of 113 recorded.

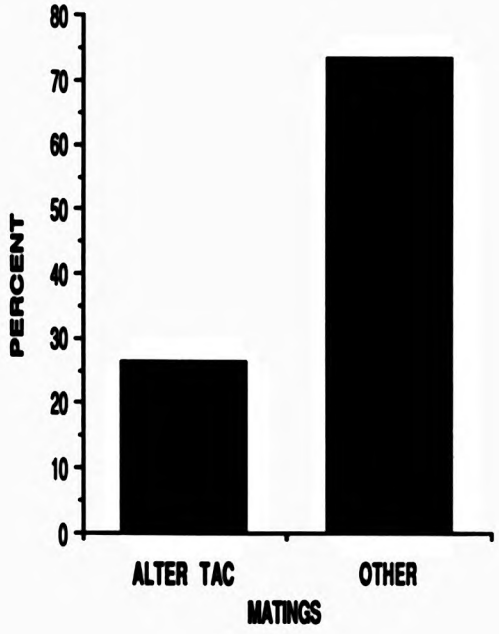


FIGURE 9.2. Percentage of alternative tactic matings observed out of the 19 matings recorded without sexual interference.

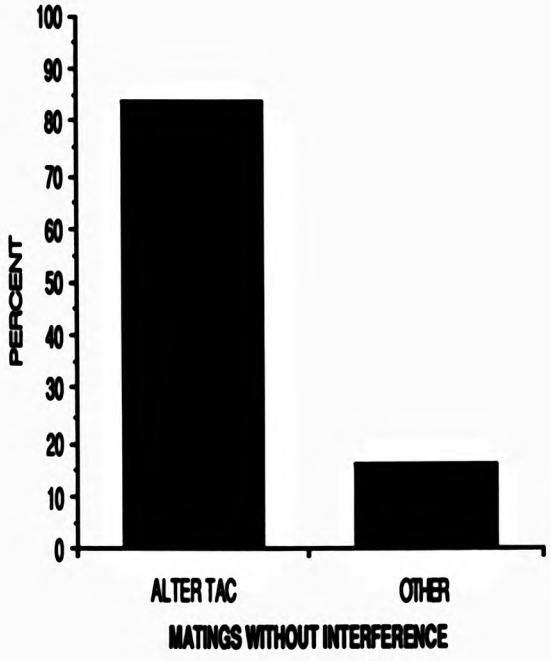


FIGURE 9.3. Percentage of the 30 recorded alternative tactic matings receiving sexual interference compared with the percentage receiving interference among the 83 other matings.

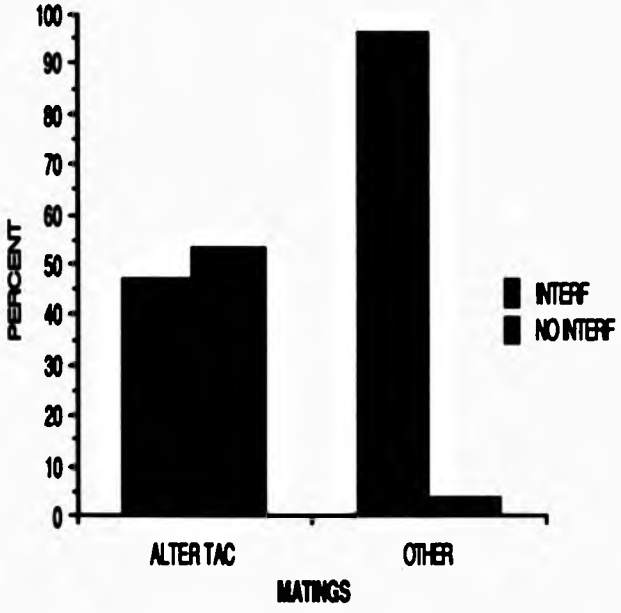
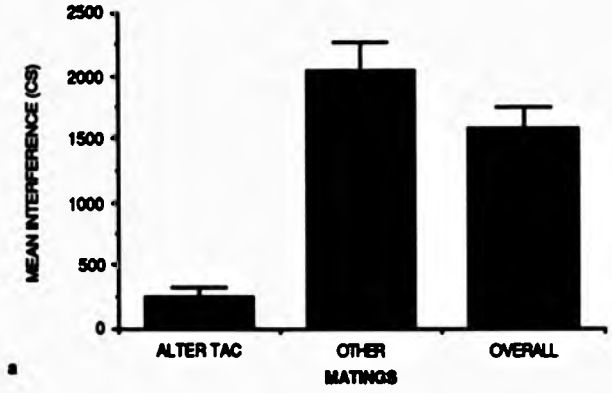
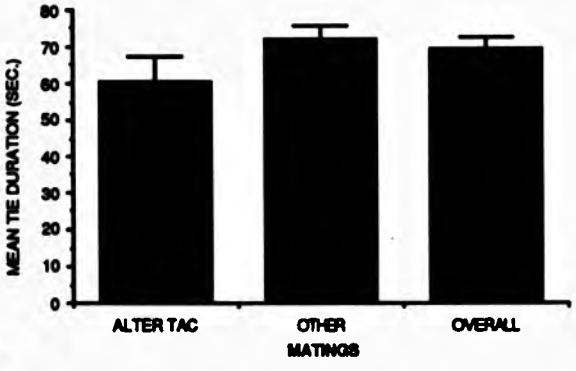


FIGURE 9.4. (a) Average amount of sexual interference per mating (determined by combined score) for the 30 alternative tactic matings opposed to the 83 others. (b) Mean tie duration per mating for the same two groupings. The overall averages are also provided. T-bars represent top half of Standard Error.



a



b

variation between the two also exists, but not as great. An average tie duration for an alternative tactic mating was 60.1 seconds, while an average tie for a normal mating was 72.3 seconds (Figure 9.4b). The difference between the two was not significant (Mann-Whitney U test, z= -1.33, p= .183, 2-tailed).

Specific

When the amount of sexual interference and duration of ties are compared between the two categories of alternative tactic matings themselves, differences also exist. The respective values of both interference and ties were less for male hide-and-hurry matings than they were for female leave. Specifically, the mean combined score of interference for male hide-and-hurry was 230.3, compared with 276.5 for female leave (Figure 9.5), and the average tie duration for the male tactic was 41.7 seconds, opposed to 69.3 seconds for the female tactic (Figure 9.6). Neither of these differences, however, were large enough to be significant (Mann-Whitney U tests, z= -.607, $p > .05$, 2-tailed and z= -1.49, p= .136, 2-tailed, respectively).

When again considering the amount of interference for both categories of alternative tactic matings, variations exist among individuals as well. The average amount of interference received by female leave matings ranged from zero for Elena to 750.0 for Bruja, and the mean received by male hide-and-hurry matings ranged from zero for Roberto, Bruno, and Flan to 800.0 for Tigre. The scores of the other individuals for both tactics fell at various levels in between (Figure 9.7a and b). No statistical tests of significance were calculated because of the small sample sizes.

Tie durations showed similar variations among individuals when comparing both categories of alternative tactic matings. With female leave

FIGURE 9.5. Average amount of sexual interference per mating (determined by combined score) for both the 19 female leave and 11 male hide-and-hurry matings. T-bars represent top half of Standard Error.

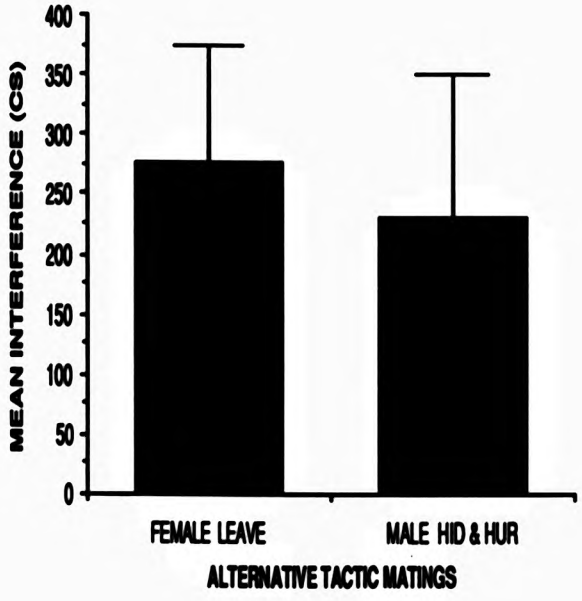


FIGURE 9.6. Mean tie duration for the 19 female leave and 11 male hide-and-hurry matings. T-bars represent top half of Standard Error.

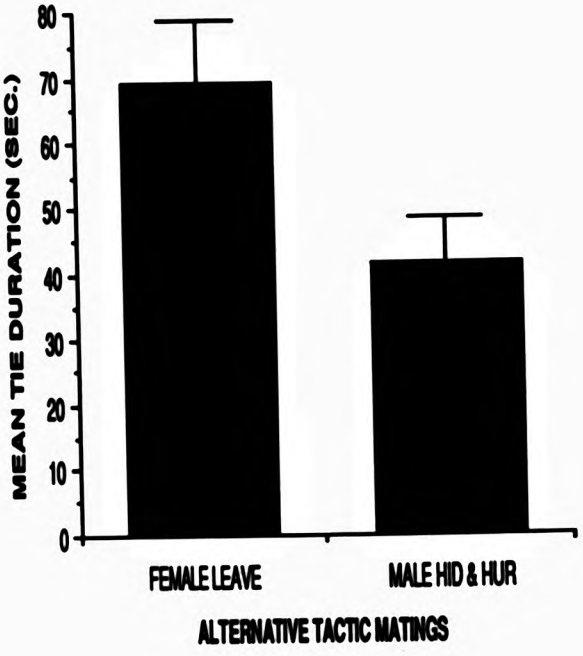
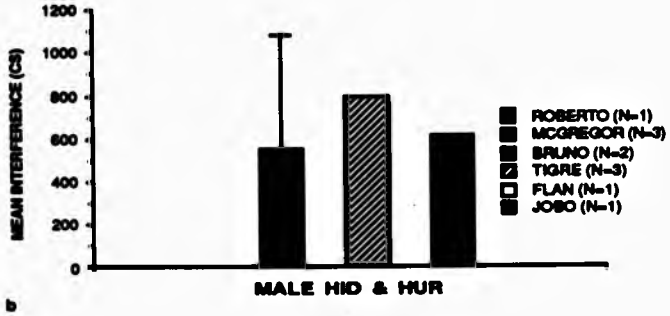


FIGURE 9.7. Differences among females(a) and males(b) in the average amount of sexual interference received per mating (determined by combined score) for the two types of alternative tactic matings. Blank columns represent matings without interference. T-bars represent top half of Standard Error.

a



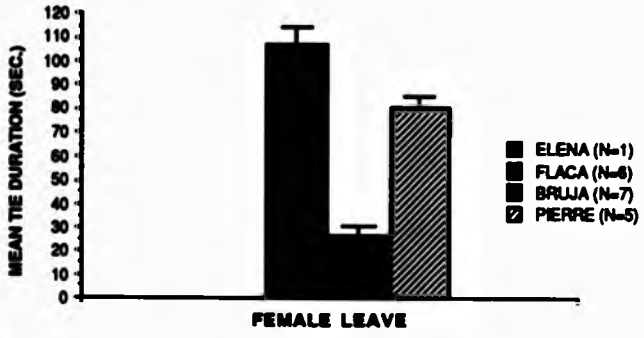
b

matings, mean individual durations ranged from 26.4 seconds for Bruja to 108.0 seconds for Flaca. Pierre's average duration was 81.2 seconds, while a tie length for Elena's single mating was not recorded (Figure 9.8a). Individual durations for male hide-and-hurry matings ranged from 25.0 seconds for Bruno to 54.0 seconds for McGregor. Tie durations for Roberto and Jobo's matings were not recorded, and Tigre and Flan's durations fell in between the high and the low (Figure 9.8b). Again, tests of significance were not run because the sample sizes were too small.

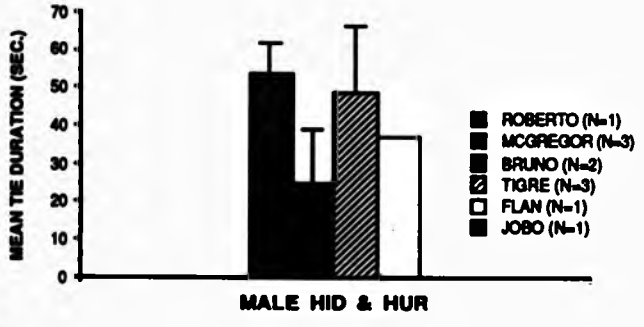
REPRODUCTIVE DATA

Even though reproductive data on males mating alternatively are not available, such data are available for females. However, these data are not readily comparable because of age differences between subjects. To make them comparable, several things were necessary. First the total number of offspring produced by each of the 3 females (Flaca, Bruja, and Pierre) who were observed to mate alternatively on more than one occasion were obtained (see Table 8.2). Second, the number of months available to these same females for reproducing was calculated by totalling the number of months that had elapsed from each of their births through March, 1987 (the last birth records presently available). Third, to obtain the mean number of months between births, each female's monthly score was divided by her total number of births. Then, the mean number of months between births for the females as a group was obtained by calculating a mean monthly score and dividing it by the total number of subjects. This resulted in an average of 1 birth for every 33.8 months. When the same calculations were performed on the 7 females who did not mate alternatively (Elena, Ucilia, Fanny, Lucia, Rosy, Canela, and Flossie), they as a group averaged 1 birth

FIGURE 9.8. Differences among females(a) and males(b) in mean tie duration for the two types of alternative tactic matings. Blank columns represent the absence of information. T-bars represent top half of Standard Error.



a



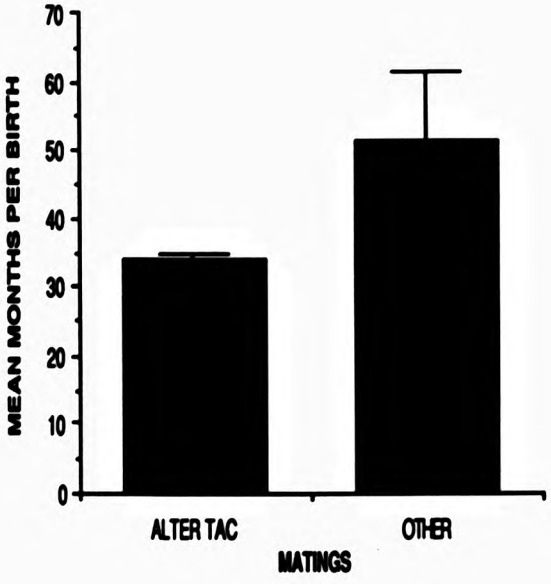
b

for every 51.5 months. Both figures are presented in Figure 9.9. The difference between the two is nonsignificant (Mann-Whitney U test, z= -1.37, p= .170, 2-tailed). However, there is a trend for shorter interbirth intervals for females who mate alternatively, and, again, it should be remembered that trends may ultimately contribute to overall fitness (Silk, 1987).

THE RETURN-BENEFIT SPITE HYPOTHESIS

As with the spite hypothesis, the hypothesis of return-benefit spite was briefly outlined in Chapter 5. Basically, spite with a return-benefit, similar to altruism with a return-benefit, postulates that even though an act performed by a perpetrator is potentially costly at the time in terms of ultimate reproductive fitness, it may eventually serve to accomplish a relative net benefit for the actor compared to the recipient. The benefit is gained if, sometime in the future, a second directly beneficial act occurs (e.g., alternative tactic mating) which does more than counter-balance the cost that the initial act originally incurred (Trivers, 1985). In other words, spiteful behaviour can be selected for especially if combined with a second act which ultimately provides a net return for the actor. Strictly speaking, as pointed out in the last chapter, if this occurs, the original act of spite should then be considered only a delayed act of selfishness. However, such reasoning creates a problem. When viewed in this restricted manner, all social behaviour, including spite, altruism, as well as cooperation, become selfish by definition, and, in reality, this is clearly not the case. All three, plus selfishness, exist because the relative gain acquired by the perpetrator of such an act (be it in net reproductive benefit or cost) always equals or exceeds that acquired by the recipient. Therefore, again, spiteful behaviour,

FIGURE 9.9. Average number of months between births for the 3 females who practiced alternative tactic matings compared with the 7 who did not. T-bars represent top half of Standard Error.



even if not recognised as such, should be selected for on its own [e.g., kidnapping attempts of neonates by unrelated females within macaques (Silk, 1983)], and, if associated with a return benefit, the chances of this should be increased. Some social behaviour may not be recognised as spiteful because of the "...unrealistic 'panmixia' of the classical model..." which implies random mating (Hamilton, 1971). So, when considering alternative interpretations of behaviour, it may be well to remember: "There is already a trend toward renaming all forms of altruism [spite] that can evolve as 'genetic selfishness,' which presumably reserves the term altruism [spite] for anything that can't evolve" (Wilson, 1980).

But what does all this have to say about the behaviour of sexual interference in stumptail macaques? It is proposed that not only has sexual interference in stumptails been selected for because it has the potential of imposing an equal or greater net loss in reproductive fitness on the recipient compared with the perpetrator of the act (spite, see Chapter 8), but interference has also been selected for because the opportunity exists within the social context of stumptails which allows it to be potentially associated with a return benefit (return-benefit spite).

Predictive Tests

If return-benefit spite can explain the phenomenon of sexual interference in stumptails, what then should be expected from the alternative mating data presented above? Predictive tests are as follows:

(1) *Results:* Alternative mating behaviour should be present allowing those of lower dominance rank to acquire return benefits.

(2) ***Results:*** If sexual interference is stressful, pairs mating alternatively should attempt to avoid interference, thereby reducing the amount of stress experienced, while at the same time possibly increasing the likelihood of conception.

(3) *Results:* Again, if interference imposes stress on mating pairs who, in turn, respond by increasing their tie durations, then the ties of alternative matings should, on average, be less than those of normal matings.

(4) *Reproductive Data:* And finally, those individuals of lower dominance rank who chose to mate alternatively should, on average, be more reproductively successful (in terms of number of offspring produced) than those who only chose to mate normally.

DISCUSSION

Evidence

Results

Predictive Test 1. Obviously, from the results presented, alternative tactic matings do exist. As shown in Figure 9.1, they comprise 26.5% of

all the matings recorded. Just under two-thirds of these were practised by females (female leave matings), while slightly over one-third were practised by males (male hide-and-hurry matings). This does not mean, however, that lower-ranking individuals using alternative matings will successfully reproduce. But, those individuals who do mate alternatively at least have the opportunity, especially lower-ranking males.

Predictive Test 2. If these matings are to be successful, assuming that social stress decreases the rate of conception and sexual interference causes stress, then it seems reasonable to expect that those practising such tactics will try and avoid occasions when interference will most likely occur: in view of other group members. As a consequence, the amount of interference received by alternative matings should be reduced.

When reviewing the data, this appears to be what happens. The average amount of sexual interference received by alternative matings was only about an eighth of that received by matings which were normal (Figure 9.4a), and the difference between the two was highly significant. It does seem reasonable then that the immediate purpose of those individuals who practice alternative matings is to mate without disturbance. I suggest the ultimate purpose is to increase their chances of reproducing by reducing the possible stress caused by interference which, in turn, may decrease the possibility of conception.

Predictive Test 3. As revealed in the last chapter, tie durations were significantly longer overall when matings were interfered with than when they were not (Figure 8.3). Tie durations occurring in the second half of a mating series were also significantly longer than those occurring in the first half of a series (Figure 8.4). The possible reason for both these circumstances is that sexual interference causes stress which, in turn, encourages males to lengthen their ties by an average of 56% in the former

circumstance and 23% in the latter. But how does this relate to alternative tactic matings? Since the purpose of mating alternatively appears to be the avoidance of interference, as noted above, the need for males to respond by extending their ties should become unnecessary. Therefore, the average tie for alternative matings should be less than the average tie for those matings that are normal. As it turns out, the average tie for the 30 alternative matings was 60.1 seconds, while the average tie for the 83 others was 72.3 seconds (Figure 9.4b). In other words, ties of alternative matings average 83% of normal matings. This is not significantly less when alternative matings are considered overall, but when they are divided into those that received interference and those that did not (46.7% and 53.3%, respectively), important differences appear (Table 9.1). It seems from Table 9.1 that when those individuals who mated alternatively were successful in avoiding interference, the duration of their ties dropped dramatically. Conversely, when they were unable to avoid interference, their ties were correspondingly and significantly longer, as were ties of normal matings with interference (Mann-Whitney U tests, $z=-2.078$, $p=.038$, 2-tailed and $z=-2.510$, $p=.012$, 2-tailed, respectively). So, it not only looks like the purpose of mating alternatively is to avoid interference, if possible, but longer tie durations are a mating males response when interference can not be avoided. Again, this may be because sexual interference is stressful.

Reproductive Data

Predictive Test 4. The final predictive test concerning individuals who mate alternatively suggests that those of lower dominance rank who do should have a higher reproductive rate than those of lower rank who mate normally. As mentioned earlier, only females can be considered here

TABLE 9.1. Matrix of mean tie durations for alternative and normal matings with and without sexual interference.

	With interference	SE	Without interference	SE
Alternative	76.2	10.1	45.5	8.8
Normal	71.8	3.6	53.0	16.0

because data on paternity is not available. But from the information presented, there does appear to be a trend toward longer interbirth intervals which may ultimately result in a higher rate of reproduction for those females as a group who do mate alternatively. The reason for this may be that by mating alternatively females avoid or at least reduce the amount of sexual interference they commonly experience while mating normally. Females who only mate normally appear as a group to have longer interbirth intervals which may lead to a lower long-term rate of reproduction (Figure 9.9). But, again, further research is required to claim anything more definitive.

REPRODUCTIVE VALUE OF SPITE WITH A RETURN-BENEFIT?

Stated simply then, and to encourage further research, it is suggested that those individuals, especially those of lower rank, who practice both sexual interference and alternative mating should gain more reproductively overall than they would otherwise, or than those who practice one or the other or neither of these tactics.

CHAPTER 10

DISCUSSION AND CONCLUSIONS

If the return-benefit spite hypothesis does explain the phenomenon of sexual interference in stumptail macaques, as this thesis preliminarily suggests, how can it explain the difference between the sexes, as shown in Chapter 7. In other words, in this free-ranging and ecologically valid study, why do males interfere significantly more than females? This and other questions pertaining to both stumptail interference and mating will be addressed in this chapter. The chapter will also provide some basic thoughts on sexual interference and mating together, attempting to place them in an evolutionary context reasonable for stumptails. It will then conclude. But, before proceeding, it should be stated that most of what follows in the discussion section is untested, and little or nothing has actually been scientifically proven. Its purpose is to hopefully encourage further thought and research using the framework this thesis has attempted to provide.

DISCUSSION

Sexual Interference

In this and other behavioural studies of stumptails (e.g., Estep et al.,

1984, 1988; Niemeyer and Chamove, 1983; Gouzoules, 1974), the alpha male of the group appears to do most of the mating. Other, less dominant males are observed to mate, particularly the beta male, but, when compared with the alpha, their amount of participation remains quite low. Females, on the other hand, mate frequently, regardless of their dominance status. As in other studies, this study found female rank order and frequency of mating to be uncorrelated. Since reproductive success is a relative matter, it seems reasonable to assume that males have more to lose when competing with the alpha male than do females competing with more dominant females. In other words, males should be expected to interfere more to reduce the alpha male's (and possibly the beta male's) overall success compared with their own. Females, who mate regardless of their position in the dominance order, should interfere less. Data in this study does support these conclusions.

Furthermore, when males and females were placed in their own respective age categories, differences in the amount of interference displayed among sub-groups were found as well. As again noted in Chapter 7, subadult males interfered the most, followed by subadult females, adult females, and then adult males. Juveniles and infants of both sexes interfered least. So, the obvious question is, why is sexual interference in this free-ranging study, at least, expressed as it is?

I propose that subadult males (e.g., Figure 10.1) provide just over one-third of all the interference observed for two reasons: first, these males, because of their sex, have more to lose reproductively over a life-time than any group of females, regardless of age, and second, since they are not fully competitive, their actions are less likely to be retaliated against by the more dominant adult males who mate. The latter reason is supported by the fact that adult males rarely interfere. Consequently, subadult males

FIGURE 10.1. Blair interfering.

have little to lose but lots to gain by trying to suppress the reproductive efforts of the dominant males, and their rate of interference is high. Also, the likelihood of any one male in this category eventually reaching alpha status is probably quite small, so again, the more they interfere at this stage, the more reproductively competitive they become. But what about adult males who are not of alpha or beta status? Should they not also interfere at a high rate to help themselves be more reproductively competitive, since their potential is, likewise, quite low. Actually, one would think they should, but the reason I propose they do not is, unlike subadult males, they provide a direct source of competition for the dominant males who do most of the mating, so the benefit gained by interfering more intensely than they already do would be quickly outweighed by the cost of being retaliated against by these same dominant males. Therefore, their approach should be to mate alternatively, which, as shown in the last chapter, they do.

However, this does not explain why females interfere, especially subadult females, whose rate of interference is second only to that of subadult males. I suggest that subadult females, as well as adult females, interfere for reasons similar to adult and subadult males; relative long-term reproductive success usually depends on a high degree of intrasexual competition. Subadult females may be somewhat more willing to suppress others by interfering than adult females because they are less sexually attractive to dominant males (Smuts, 1987), which places them at a slight reproductive disadvantage. Subadult females can, of course, mate alternatively with less dominant males, as they sometimes do, but their likelihood of conceiving in this manner is probably less compared with mating conventionally, which they are unlikely to do. So, they interfere at a higher rate to compensate. In contrast, adult females, since they are

attractive to dominant males and are already reproducing, do not need to suppress others as much, but the need exists none the less. If they can hoard sperm from fit (dominant) males for themselves (Small, 1987) and resources for their present and future offspring (Hrdy, 1977) by suppressing the reproductive efforts of others by interfering, then they should certainly be selected by evolution to do just that.

In addition to sexual interference itself, other circumstances reflect the reproductive competitiveness of adult and subadult female stumptails. Two examples follow:

> *On two separate occasions, shortly after Lucia had mated with Pancho, Pierre and Ucilia together threatened Lucia, even soliciting Pancho for help. Just previous, both Pierre and Ucilia had sexually interfered with Pancho and Lucia. Furthermore, on four other occasions, a more dominant female approached one of lesser dominance, forced her to present her hindquarters, and then proceeded to finger and sniff her vagina. On two of these occasions, the recipient had either just mated, or mated sometime that day. Twice, the perpetrator was Pierre who was involved in the threatening incidents sighted above and who was also an intense intruder.*

Interference by immatures, on the other hand, is traditionally explained by two standard hypotheses (Chapter 8). The first, parent-offspring conflict, is an ultimate explanation, and is attributed to Trivers (1974), though not specifically in the interference or primate context (e.g., Tutin, 1979). This hypothesis proposes that interference with the matings of one's mother by immatures demonstrates a predictable conflict in how the

maximisation of inclusive fitness (Hamilton, 1964) should be distributed. The offspring seeks to garner as many resources (e.g., maternal care and milk) as the mother can provide. At the same time, it is in the reproductive interest of the mother to set a limit on these resources in order to conceive and begin providing for her next offspring. Accordingly, the stage for conflict of interest is set, and interference to prevent mating follows.

The second explanation of why immature primates sexually interfere is for the proximate reason of observational learning (e.g., de Benedictis, 1973). This hypothesis proposes that immatures are attracted to mating simply to learn how to perform sexually as adults. In other words, the more they observe and interact, the more sexually proficient they later become.

But how do either of these explanations apply to stumptails? The second seems difficult to accept because in many primate species where sexual interference among immatures is uncommon, or altogether nonexistent, later sexual functioning readily develops (e.g., in rhesus macaques). There seems no need then to call upon observational learning to explain interference by immatures in stumptails. But the first explanation of parent-offspring conflict is also improbable. Even though juveniles and infants interfere more intensely in their mothers' matings than they do in the matings of unrelated females, as noted in Chapter 7, I propose that mere proximity can account for this correlation. It does appear, when referring to Table 7.4, that immatures are more highly affiliated with their mothers than any other individual pairs. If it is ultimately reproductively beneficial for an immature to spite the matings of others by interfering (in adult and subadulthood), then this same behaviour should be selected for in the earlier stages of development to insure the future competitiveness of the individual. (They may also be interfering on behalf of their mature kin.) So, whatever

the minor costs are in inclusive fitness that immatures may incur by interfering in the matings of their mothers, they will soon be repaid by the greater costs these same, yet older, immatures possibly impose on unrelated individuals by interfering in their matings even more intensely. Consequently, I suggest that interference is spiteful from its earliest development.

A different question now needs asking: why not cheat? In other words, in a simultaneous but independent group activity such as sexual interference in stumptails, why not simply not interfere and let others incur all the potential costs involved? This does not make sense because if one individual cheats by not interfering (if interference and conception are linear), then the chances of a competitor successfully reproducing are that much greater than if this same individual had interfered. It may not make much difference for one, but if several individuals cheat by not interfering, then the likelihood of a mating pair reproducing is increased. If they do reproduce, then everybody, except the pair and their few close relatives, loses. Selection should favour noncheaters, which, from the data, it appears to have done.

Mating

The focus now will turn to several aspects of the stumptail mating pattern that have yet to be explained. These are the lack of an obvious sex skin by females in oestrus, the pattern of a single mount to ejaculation (SME) by males, the apparent lack of consortships between males and females during oestrus, and, lastly, the apparent nonseasonality of mating. In other words, why do these patterns exist in the stumptail behavioural repertoire over other patterns more common in other species of macaques, as revealed in Chapter 6 and summarized in Table 6.1? I propose that all

may be interrelated with sexual interference, and this section briefly presents hypotheses.

If sexual interference in stumptails is as reproductively disruptive as this research speculates, then evolution should select for those individuals who will, through both anatomy and behaviour, be the least effected. It may be that those females who are better able to avoid attracting attention while in oestrus are also the females who are best able to avoid having their matings interfered with. Accordingly, I suggest that a likely evolutionary reason for the lack of an obvious sex skin in female stumptails is to avoid attention and not be interfered with by others while mating.

Similarly, the SME mating pattern used by male stumptails may accomplish the same end. Hypothetically, all other things being equal, if male stumptails do require more than a single mount to reach ejaculation, other group members would have more time to be in a position to interfere with their matings. In order to help prevent this, selection may have favoured the SME pattern. Other unknown pressures were probably responsible for developing the same pattern in other macaques where it occurs (e.g., Bonnet and Barbary macaques), but, in stumptails, I suggest that sexual interference may have been the selective force responsible.

Furthermore, consortships, which are common among all other species of macaques, are absent among stumptails. But why in this behaviour (or lack of) should stumptails stand alone? First of all, like highly developed sex skins in female primates and multiple mounts to ejaculation (MME) in males, consortships in macaques may attract attention, and, hence, lead to interference in stumptails. What I suggest is that consortships did not evolve as part of the stumptail mating pattern for the simple reason that those individuals in the distant past who chose not to mate while in consort were possibly the same individuals whose matings were interfered with the

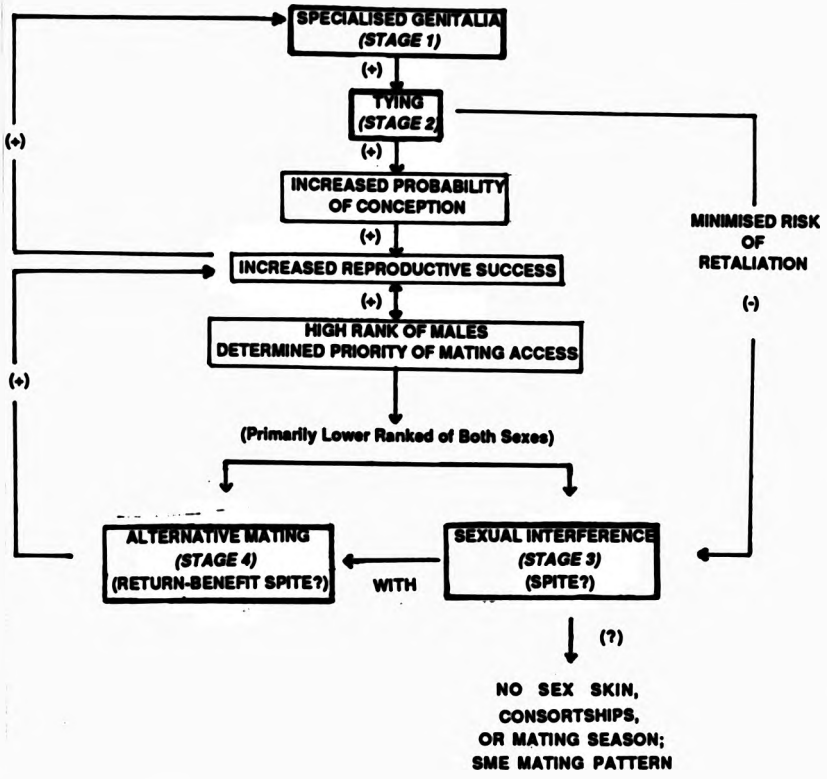
least. As a result, they left the greater number of offspring to continue the practice which ultimately led to the pattern observed among stumptails today: no consortships.

The same explanation can be forwarded for the absence of a mating season among stumptails. The ancestral individuals who mated outside the context of a traditional mating season may have been those who best avoided attention and, in turn, best avoided sexual interference. Possibly out reproducing all others, the nonseasonal mating pattern of these individuals became standard. Again, as with the SME pattern above, different pressures were probably involved in selecting for nonseasonality of breeding in other species of macaques.

SEXUAL INTERFERENCE AND MATING

So where does all this leave us when considering the phenomenon of sexual interference in stumptail macaques? In other words, in the overall context of stumptail history, why did sexual interference develop and how does it fit? This section will attempt to answer these questions by presenting a brief overview of what I propose is a likely scenario of the evolutionary development of the important characteristics of the stumptail mating pattern. I suggest they evolved by sexual selection and developed in four interconnected stages: the first two structural and the latter two behavioural. Each are presented below in their proposed developmental sequence. Figure 10.2 provides a summary.

FIGURE 10.2. Summary of the proposed evolutionary stages of stumptail mating? Minus and plus signs represent costs and benefits, respectively.



Evolutionary Stages of Stumptail Mating?

Structural

Stage 1. ***Specialised Genitalia Evolved to Encourage Tying?*** As outlined in Chapter 6, the genitalia of both male and female stumptails are quite different anatomically from those of other species of macaques. To date, speculation as to why has been minimal. Fooden (1967) suggested that it may have been to prevent hybridisation with other sympatric species of macaques, but he said nothing as to why this should have occurred only in stumptails. On the other hand, Dixson (1987b) suggested that sexual selection is a more likely explanation.

I propose that what is now agreed to be a significant anatomical difference in the genitalia of sumptails can be traced to an added success in reproduction. In other words, beginning at one time in the history of the development of the stumptail mating pattern, and continuing thereafter, individuals with slightly altered sex organs, reminiscent of those of stumptails today, were able to out-produce their contemporaries. Basically, the altered genitalia was conducive to prolonged intromission, referred to as tying. This led to the second stage.

Stage 2. ***Tying Evolved to Increase Conception?*** Compared with other species of macaques, the fact that tying exists in stumptails, regardless of the cause of its origin, is unique. It occurs rarely among primates, of which the greater galago *(Galago crassicaudatus)* is an example (Dixson, 1976). Among stumptails and greater galagos, both in which the males possess extended baculum length and cone-shaped projections on the glans and corpus penis, it has been speculated that tying has the likely function of increasing the probability of conception (Dixson, 1987b).

In the evolutionary scenario of the development of stumptail mating, I

suggest that this may be what happened. Individuals who had altered genitalia also had prolonged periods of post-ejaculatory intromission which encouraged insemination and, in turn, increased their rates of reproduction. With this development being selected for and eventually becoming common, the circumstances were then set for Stage 3.

Behavioral

Stage 3. ***Sexual Interference Intensified to Counter Increased Reproduction?*** Since the reproductive success of any particular individual is always relative to the success of others, an increase in reproduction by one's competitors must not go unchallenged. But how does one challenge those of higher rank where dominance has already been established as the constraint-free system for establishing priority of access, and in this case, priority of access to partners with which to mate?

I suggest that this may have been the position that ancestral stumptails of lower rank found themselves. For them to even mildly succeed, circumstances dictated that alternative approaches had to be pursued, and as it turned out, one of these was to sexually interfere in the matings of competitors, and particularly the matings of males of high rank who invariably seem to dominate. Tying made this possible by decreasing the probability of being retaliated against. But other tactics were also involved, and this leads to the final stage of the scenario, Stage 4.

Stage 4. ***Alternative Tactics in Mating Expanded to Further Competition in Procreation?*** Sexual interference is obviously an indirect component to reproductive success. But for individuals of lower rank to compete successfully with those of greater dominance, mating must occur, with alternative methods substituting for priority of access.

I suggest that historically stumptails of lower rank were able to mate

successfully by choosing one of two approaches depending on their sex: females led their male suitors off from the group before mating, while males mated with cooperative females surreptitiously. The immediate purpose of individuals practising either tactic was possibly to avoid receiving sexual interference. The ultimate cause may have been for them to acquire a return benefit by successfully reproducing. Accomplishing the first made the second more probable, and I suggest that this is why alternative tactics, and sexual interference in particular, continue as part of the stumptail mating pattern today.

CONCLUSIONS

To conclude, what has this first free-ranging study of stumptail macaques discovered about sexual interference? Several new findings have come to light, including:

(1) Sexual interference in stumptails seems to be as much a part of their social structure in a free-ranging setting as it does in captivity.

(2) There appears to be a direct and positive association between the amount of sexual interference matings receive and the duration of their ties: the greater the amount of interference, the longer the ties.

(3) A trend may exist whereby males require more mounts on average to reach ejaculation when their matings are interfered with than when they are not.

(4) Lifetime reproduction for some females may be inversely correlated with their dominance rank.

(5) Females may employ a competitive reproductive tactic labelled female leave.

(6) Alternative matings (female leave and male hide-and-hurry) appear to receive significantly less sexual interference than normal matings.

(7) Tie durations of alternative matings without sexual interference are significantly less than either alternative or normal matings with interference.

(8) Most matings that are not interfered with are alternative matings.

In addition, this thesis has described a holistic and evolutionary framework for the development of sexual interference, a framework which possibly explains this phenomenon better than the three captive studies have done. However, this theoretical framework has not been proven as the explanation of sexual interference. But future research into the possible stressful effects sexual interference has on matings and the contribution alternative mating provides towards successful reproduction would better access its contribution. Paternity data would be useful for both. A more open consideration of the possible use of spite as a supplemental reproductive tactic by highly intelligent and socially discriminating beings would also help. I wish to encourage further thought and empirical research

on all three. So, to return to the question posed in the title (*Is sexual interference in stumptail macaques return-benefit spite?*), only time will tell.

APPENDIX

TERMS AND DEFINITIONS OF BEHAVIOUR BY CATEGORY*

CATEGORY	*BEHAVIOUR:* DEFINITIONS
M,SI,D	*Approach:* Walking toward another.
M,SI,R,D	*Avoid:* Locomoting away from another at a walking pace while staring.
M,SI	*Bared Teeth:* Exposing the teeth either parted or together by retracting the lips while gazing alternately between fixation and avoidance.
SI	*Bark:* High intensity vocalisation of short duration.
SI,R,D	*Bite:* Gripping another's flesh between the teeth.
M	*Bite (Pre-Mount):* As above but prior to mounting.
M	*Bite (Post-Mount):* As above but following mounting.
M	*Bite (Post-Ejaculation):* As above but following ejaculation.

* Adapted from Bertrand (1969), and listed in alphabetical order. Letters represent categories in which these behaviour can occur as follows: M=mating, SI=sexual interference, R=retaliation, A=affiliation, D=dominance, O=oestrus. See Chapter 4 for category definitions and protocols.

SI	*Bounce:* Involves rapid vertical motion while remaining in one place.
SI	*Branch Shake:* Bouncing on a tree limb rapidly and repetitively.
M,R	*Break Tie:* Withdrawing the penis from the vagina within 15 seconds of ejaculation.
SI,D	*Charge:* Moving rapidly toward another resulting in contact.
SI,R	*Chase:* Rapidly succeeding another as he or she recedes but without contact.
SI	*Climb On:* Moving from a substrate position onto another by grasping his or her body hair and uplifting.
SI	*Cling To:* Grasping and hugging the hair and body of another with both hands.
SI	*Close By:* Within 1 m of another.
M	*Collapse:* Female changing from quadrupedal stance to ventral ground- surface contact.
M,SI,R,D	*Cower:* Leaning away and hunching while staring at another.
SI	*Distant:* Beyond 5 m of another.
O	*Face Colour:* Noticeable change in female's facial colour.
SI,R	*Face-To-Face:* Placing the face within 20 cm of another.
O	*Female Follow:* Male succeeding female at walking pace.

O	*Female Groom:* Female carefully picking through or slightly brushing aside male's hair.
M,O	*Finger:* Inserting a finger into a female's genital canal and smelling upon extraction.
R,D	*Flee:* Running from another.
M	*Flee (Pre-Mount):* As above but prior to mounting.
M	*Flee (Post-Mount):* As above but following mounting.
M	*Flee (Post-Ejaculation):* As above but following ejaculation.
M	*Follow:* Succeeding another at a walking pace.
M	*Frown-Round-Mouth:* Same as round mouth with widening of the eyes, lowering of the brow, and raising of the forehead. Often accompanied by body tenseness and rhythmic vocalisations in the male. Synonymous with ejaculation.
SI	*Genital Display:* Exposing the genitalia to another: Female by standing quadrupedally with either of her legs raised or extended, and male by bipedally facing forward.
M,R,D	*Glance Away:* Avoiding eye contact with another
M,SI,R,D	*Grab:* Clasping another's hair or flesh with one or both hand(s).
M	*Grasp Haunches:* Holding another's hindquarters.
M,SI,R,D	*Grimace:* Retracting the lips vertically while drawing the corners of the mouth back exposing the teeth and flattening the ears.

A	*Groom:* Carefully picking through or slightly brushing aside another's hair with one or both hand(s).
M	*Groom (Pre-Mount):* As above but prior to mounting.
M	*Groom (Post-Ejaculation):* As above but following ejaculation.
M,SI,R,D	*Grunt:* Short, harsh, low-pitched vocalisation.
M,SI	*Hair Erection:* Erection of the body hair in the areas of the neck, shoulders and upper back.
M,SI,R,D	*Hit:* Striking another with one or both hand(s).
M,R,D	*Hold:* As above but for a minimum duration of 5 seconds.
R,D	*Hop:* Bouncing rapidly away from another.
A	*Huddle:* Includes one or both of the following: *Chin-On-Nape:* Resting the chin on the nape of another's neck. *Nestle:* Clinging with another ventro-ventrally or dorso-ventrally.
SI	*Jump On:* Propelling through the air and landing on another.
M	*Leave:* Moving away from another beyond 5 m.
M	*Lift Rear:* Raising another's hindquarters without his or her cooperation.
M,SI	*Lip Smack:* With the mouth closed, protruding the lips forward forming a puckered expression, raising and lowering the mandible rhythmically, and alternately extending and retracting the tongue.

M	*Look Back:* Female orienting her head and eyes toward the male during mating.
SI,D	*Lunge:* Moving quickly toward another but halting abruptly before contact.
O	*Male Follow:* Female succeeding male at walking pace.
O	*Male Groom:* Male carefully picking through or slightly brushing aside female's hair.
SI	*Masturbate:* Manipulating the genitalia.
M	*Mount:* Grasping a female's hindquarters with one or both hands, her hindlegs with one or both feet, and then standing erect. Male simultaneously inserts his penis into the female's vagina.
SI	*Mount (Pair Member):* Climbing onto a member of a mating pair and thrusting.
SI	*Mount (Other):* As above but the addressee is not a member of a mating pair.
SI,R	*Mouth-To-Mouth:* Placing a slightly opened mouth onto the mouth of another.
SI	*Near By* : Within 1-5 m of another.
M,SI,R,D	*Open Mouth:* Intensely fixating on another while opening the mouth slightly to fully, as the corners remain natural, and alternately raising and lowering the brow.
M	*Pant:* Rapidly inhaling and exhaling air through an open mouth.

M,A,O	*Passive Contact:* Contacting another without further social interaction.
SI	*Peer-At-Genitals:* Placing the face within 30 cm of another's genitals while staring.
O	*Perineal Colour:* Noticeable colour change in the perineum.
SI	*Play Face:* Opening the mouth slightly to fully with the corners remaining natural.
SI	*Pout Face:* Protruding the lips while closing or slightly opening the mouth forming an "O" shape without exposing the teeth.
M,SI,R,D,O	*Present:* Orienting the hindquarters toward another while standing quadrupedally.
M,A,O	*Proximity:* Standing or sitting within 1 m of another without contact.
M,SI,R	*Pull:* Forcibly tugging by gripping another's hair or flesh with one or both hand(s) and retracting.
M	*Pursue:* Succeeding another at a pace slightly more rapid than a walk.
M,SI,R,D	*Push:* Extending to another followed by self-propulsion.
SI	*Reach:* Extending either arm toward a mating pair.
M	*Reach Back:* Female extending either arm toward the male while mating.
SI,R	*Redirect Aggression:* Threatening or attacking another upon being threatened or attacked.

M	*Remained Mounted:* Continuation of the pre-ejaculatory mating position.
SI,R,D	*Roar:* Long, harsh, high-pitched vocalisation.
M,SI,R,D	*Round Mouth:* Intensely fixating on another while drawing the ears forward, opening the mouth slightly, and bringing the corners forward forming an "O" shape.
SI	*Run Around:* Racing in circles around a mating pair.
M,SI,R,D	*Scream:* Strong harmonic vocalisation of high intensity.
M,SI,R,D	*Screech:* A harsh, double-segmented, medium to high intensity vocalisation.
M	*Self-Inspect:* Visually and tactilely examining the genitalia.
M,SI,R,D	*Shriek:* Long and loud shrill vocalisation of high intensity.
M	*Sit Back:* Changing from a pre-ejaculatory mating position to a dorso-ventral sitting position.
M	*Sit Behind:* Seating behind another within 50 cm.
R	*Slap At:* Rapidly extending either arm toward another with an open hand.
M,O	*Sniff:* Investigating a female's perineum by placing the nose within 15 cm and smelling.
M,SI,R,D	*Squeak:* An intermediate to high grade shrill vocalisation.
D	*Stalk:* Walking toward another while head and shoulder bobbing and slightly changing directions.
M,SI,R,D	*Stare:* Visually fixating on another.

O	*Swelling:* Noticeable enlargement of the perineum.
M,SI	*Teeth Chatter:* Retracting the lips vertically while drawing the mouth corners back exposing the teeth, raising and lowering the mandible rhythmically, and alternately extending and retracting the tongue.
M	*Teeth-Chatter-Grimace:* As above with flattening of the ears.
SI	*Teeth Grind:* A low intensity sound produced by closing the mouth and grinding the teeth.
M	*Thrust:* Male's pelvic area moving forwards and backward while mounted.
M	*Tie:* Continuing genital intromission beyond 15 seconds following ejaculation.
SI	*Touch:* Lightly placing one or both hand(s) on another.
O	*Vaginal Bleeding:* Menstrual bleeding from the perineum.
O	*Wound(s):* Flesh alteration on female inflicted by another's bite(s).
SI	*Yawn:* Opening the mouth maximally while inhaling and baring the teeth.

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